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THE SPECIES CONCEPT

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INTRODUCTION

The species concept is focal in evolutionary studies and, indeed, in all biological thought. Its endless discussion is sometimes boring and seemingly fruitless, but is not wholly futile. In the course of such discussion the concept has been clarified, comprehension and a consensus have tended to develop, and the concept has changed in a significant way. There have recently been two more flurries of attention to this perennial topic. One, mostly in EVOLUTION, by Burma (1949a, 1949b), Mayr (1949), Dunbar (1950), Elias (1950), and Gregg (1950), was originally concerned with whether the species is a "fiction" or is "objective," but also treated such matters as the relationships of neontological and paleontological species concepts. The other, in the *Journal of Paleontology*, by Weller (1949), Jeletzky (1950), Bell (1950), and Wright (1950), was concerned with the bases and practices of paleontological systematics and also with "morphological" versus "phylogenetic" or "natural" versus "unnatural" classification. These papers, among others, and an attempt to grapple with the whole problem for a class in systematics have inspired the following remarks.

I agree with most of what all the authors just cited have said. I believe, however, that it is possible to say much of this in a somewhat different and therefore possibly clarifying way, to combine some of their apparently but not really conflicting views into one consistent statement, and to add a few significant considerations not explicit, at least, in any of their papers.

Parts of the discussions cited and some of the apparent conflicts are primarily semantic. By a ponderous application of symbolic logic, Gregg sought to show that the issue raised by Burma and Mayr is not a genuine taxonomic problem or, at least, that if it does relate to a taxonomic problem it does so in the wrong words. It is, of course, important that words be used as accurately as possible and that they do not obscure properly taxonomic questions. Nevertheless, Burma and Mayr (as well as subsequent discussants) *were* considering a genuine taxonomic problem, in words perhaps not logically impeccable but, taken in context, adequately performing their main semantic function, that of communicating understandably among colleagues.

The semantics of the systematists' vocabulary is a fascinating subject, which

surely does have its own importance but which has the danger of merely diverting attention from the systematists' proper business, systematics. I believe that most of the purely semantic confusion on the present subject can be avoided if such terms as "real," "natural," or "objective," and opposite or contrasting terms, are not applied to taxonomic categories or methods of classification, and if the two terms "arbitrary" and "non-arbitrary" are used in specially defined senses.

Definitions of taxonomic categories, such as a species, specify the sort of data or of inferences from data that are to be used in assignment of organisms to a group ranked in that category. For instance, the category definition of a species as a group of "actually or potentially interbreeding natural populations which are reproductively isolated from other such groups" (Mayr) specifies that data and inferences as to interbreeding and its absence are to be used. In some cases the data or inferences used will indicate essential continuity among the organisms to be grouped, and in other cases they will indicate essential discontinuity. Under the preceding genetic definition, actual or potential interbreeding is continuity and reproductive isolation is discontinuity. With a morphological-associational definition, continuity would be overlap in variation between compared populations and discontinuity the absence of overlap. Essential continuity or discontinuity in geographic, ecological, or temporal distribution has obvious meaning.

I propose to call taxonomic procedure arbitrary when organisms are placed in separate groups although the information about them indicates essential continuity in respects pertinent to the definition being discussed, or when they are placed in a single group although essential discontinuity is indicated. Conversely, procedure is non-arbitrary when organisms are grouped together on the basis of pertinent, essential continuity and separated on the basis of pertinent, essential discontinuity. Of course no stigma is meant to attach to taxonomic procedure thus defined as arbitrary. A completely non-arbitrary classification is impossible. It would be possible to extend discussion to such points as the precise definition of "essential continuity" or other parts of these definitions, but I think their meaning will be clear to all taxonomists, now or as discussion proceeds, and that semantics may be dropped at this point.

Typology, Morphology, and Genetical Groups

The typological concept of a taxonomic group is that the group corresponds with an abstract or ideal morphological pattern. Variation may be dealt with by a fixed or intuitive standard as to allowable deviation from the pattern, in which case the grouping is arbitrary. (It may either include discontinuities or draw a line across continuity.) Or, somewhat less naïvely, at a given level, usually that of species, the criterion of continuity in variation around the pattern may be used, a non-arbitrary procedure for that category.

The typological concept is pre-evolutionary and non-evolutionary. It still underlies a great deal of taxonomic practice but is now seldom favored in theory. Arkell (1950), an experienced paleontological taxonomist, seems to be accepting it when he says that, "Theoretically, at least, the number of species named reflects the number of forms, and so is more or less an objective matter," but he was mainly concerned with the highly laudable desire to keep super-specific categories conveniently manageable. The only serious modern theoretical support for frankly typological taxonomy comes from those few students who believe that species arise by abrupt morphological change from one "morphotype" to another, notably Schindewolf (1950).

Most of the data actually used in the practice of taxonomy are morphological. It is therefore not surprising that practical taxonomists suggest from time to time that classification should be morphologi-

cal, in principle, as Weller (1950) has recently done. But a purely morphological classification would be based strictly on degrees of morphological difference between organisms, and this is really so impractical that no one, not even Weller, really tries to do it consistently. It is a commonplace that the degree of morphological difference within what everyone, morphologist, geneticist, or other, calls a single species is frequently greater than that between what all call separate, related species. It is also quite impractical to obtain a valid, over-all measure of total morphological difference between two organisms. Characters are always selected, weighted, and interpreted. As Wright (1950) pointed out in criticism of Weller, the usual and meaningful basis for selection, weighting, and interpretation is phylogenetic. Even typological classification, more strictly morphological than others, requires definition of the morphotype from characters in a group already set up on grounds not, in practice, purely morphological. Typological or not, practical morphological classification starts with some sort of grouping and in most practice this is usually an attempt to recognize what is (whether so called or not) a genetically defined population. Thus Bell (1950) cogently argues the value of stratigraphic evidence in paleontological taxonomy because it bears on pertinent and useful biological taxonomic criteria that are not morphological.

The fundamental point here for taxonomy is the modern idea that it is populations, not specimens, that are being classified. Newell (1948) has stressed this point for invertebrate paleontology in criticism of the practice of naming variants which are not populations. Jeletzky (1950) also emphasizes this point of view and its usefulness (one might say, necessity) for phylogenetic classification, although his argument is greatly weakened by his statement that variants are "natural groups" within the population and by his contrasting of phylogenetic with statistical methods, as if statistical methods were not a means of reaching conclusions about populations and hence about phylogeny. I have also insistently recommended population concepts in taxonomy, and so have many others. A few paleontologists have been mentioned first because, on the whole, paleontologists have been rather slower to grasp or accept the population concept of taxonomic groups. Despite some conservatives and reactionaries, the concept is widely accepted among neontologists (in botany, e.g., Camp, 1951; or in zoology, e.g., Mayr, 1942).

If classification is to start with populations, category definitions at and below the species level should refer to populations which, further, should be meaningful biologically. It seems to me, and few systematists are likely now to question this, that such groups should likewise have evolutionary significance. Here is the most serious fault of typological or of purely morphological definitions. Unless by chance or unless a hidden genetical criterion is actually used, they do not define biological populations or have clear evolutionary significance.

Attention to biologically significant populations is the basis and justification for the now usual neontological definitions of the species category in terms of interbreeding and reproductive isolation, i.e. of genetical factors, like the definition already quoted from Mayr. As Wright (1950) has mentioned, the fact that a species, as a group, is actually diagnosed in morphological terms, does not conflict with definition of the species, as a category, in genetical terms. The basis for definition of a category is quite different from the evidence available for decision as to whether a particular group of organisms meets that definition. And although the evidence used is mainly morphological in practice, it also almost always includes other sorts of data as well: distribution or association, at least, and preferably also other information.

The genetical definition of a species as

a group of actually or potentially interbreeding organisms reproductively isolated from other such groups is non-arbitrary both in its inclusion and its exclusion. Its criteria are reproductive continuity and discontinuity. The group defined is co-extensive with the continuity and bounded by the discontinuity. A species under this definition is the largest group with non-arbitrary exclusion and the smallest group with non-arbitrary inclusion. By the criteria of this definition and in cases to which it applies, infraspecific groups are non-arbitrary as to what they include (being reproductively continuous, by definition), but more or less arbitrary as to what they exclude (having boundaries without full reproductive discontinuity, by definition). Under the same criteria and circumstances, supra-specific groups are arbitrary as to inclusion, because by definition they do or may include two or more groups between which there is discontinuity, but non-arbitrary as to exclusion, because their boundaries coincide with the non-arbitrary boundaries of included species.

Thus under this particular concept and in the particular cases to which it applies, the species is defined as the one taxonomic category that is non-arbitrary both in exclusion and in inclusion. This is another way of expressing what is clearly intended by statements that the species (so defined) is the "objective" or the "real" taxonomic unit. If my usage of "non-arbitrary" is accepted and discussion of the meaning of "objective" or "real" is avoided, it should not be seriously questioned that the statement of the first sentence of this paragraph is valid. Objections, which may also be entirely valid in their own terms, are of five principal sorts:

1. The genetical concept of species is not the only one possible, and for certain groups and in particular circumstances it may be less desirable than some other.

2. Application of the genetical definition to actual cases, even those to which it could theoretically apply, sometimes turns out to be vague or impractical.

3. There are many groups of organisms, or circumstances involved in their taxonomic grouping, to which the stated genetical definition does not apply even in theory.

4. The genetical definition implies but does not adequately state or overtly take into consideration more definitely evolutionary criteria on which it does or should depend, criteria as to the evolutionary role of a lineage, to be discussed below.

5. Application of this or of related evolutionary concepts of the species does not correspond with past and current usage in certain groups and by certain taxonomists.

It seems to me that all these objections have considerable force, more force than is granted them by some students whose taxonomic work is in the circumscribed fields where the genetical definition is in fact most practical or those whose interests are not primarily taxonomic. Yet I do not think that the objections invalidate the genetical concept or remove it from a central and basic position in taxonomic theory. They merely require that it be modified in certain applications and that it be supplemented by other concepts to meet situations to which it does not properly or practically apply. The rest of this paper is devoted mainly to discussion of some desirable or necessary modifications and supplemental concepts. One pertinent subject not directly discussed, because of limitations of space and ability, is the taxonomy of asexual groups, clones, apomicts, agamic complexes, and the like. Some of what is said below bears inferentially on this subject, and it has been briefly but ably considered by Stebbins (1950) with references to older literature.

Genetical and Evolutionary Species

As Mayr (1946, 1950) has emphasized, the usefulness of the genetical concept in taxonomy and the non-arbitrary defini-

tion of the genetical species (its "objective reality") are most evident in what he calls "non-dimensional species," those established in biotas living in one place at one time. Under such conditions, discontinuities in morphological and associated physiological variation are usually evident. In sexually reproducing groups it is almost always easy under these circumstances to establish by observation, experimentation, and inference which morphological discontinuities reflect reproductive discontinuities and to designate these as species boundaries.

But, as Mayr has also recognized, the fact that genetical species are usually rather obvious under these special limitations does not mean that they are equally clear and the genetical definition equally adequate under other and perhaps more important conditions. Populations do have extension in time and space and a non-dimensional taxonomy cannot cope with many essentials of life and of its evolution. With extension in space, the criteria of genetical continuity and discontinuity, of actual or potential interbreeding or its absence, cease in many cases to be absolute and clearly non-arbitrary and become merely relative. The similar and related local populations may not in fact interbreed over a period of years and yet may reasonably be considered as still having that potentiality. On the other hand, quite extensive interbreeding may occur between adjacent populations which nevertheless retain their own individualities, morphologically and genetically, so clearly that any consensus of modern systematists would call them different species. In some groups of plants, even though species are defined and considered as genetical entities, occurrence of some hybridization between adjacent species may be the rule rather than the exception. In such cases the species are in part arbitrarily bounded even though the gene flow is less between than within species, and the genus may become the most fully non-arbitrary unit (a thought expressed in other words by Camp, 1951). A rigidly genetical zoologist might then insist that such botanical genera equal zoological species, but evidently most botanists feel that in some way their species *are* analogous with zoological species and they can make out a good, even though not an absolutely clear-cut, case. (See Stebbins, 1950.)

In practice, even by zoologists who adhere strictly to genetical concepts of taxonomic units and who work on groups to which the concepts are applicable, it is often clear that the criterion of interbreeding or its absence is not taken as wholly decisive. Species may be distinguished even though they interbreed (hybridize) to some extent, and populations may be referred to a single species even though there is evidence that they are not in fact interbreeding. Other criteria are given weight additional to that of their evidence on interbreeding, e.g., morphological divergence, partial or full intersterility, and especially occurrence with discontinuity in the same area.

The genetical definition is meaningful because it is related to the evolutionary processes that give rise to the groups being classified. Yet the genetical criteria are not related to evolutionary change directly but only, as a rule, by implication. The following seems to be the strictly *evolutionary* criterion implied: a phyletic lineage (ancestral-descendent sequence of interbreeding populations) evolving independently of others, with its own separate and unitary evolutionary role and tendencies, is a basic unit in evolution. The genetical definition tends to equate the species with such an evolutionary unit. Most of the vagueness and differences of opinion involved in use of the genetical definition are clarified, at least, if not wholly resolved by taking the genetical criterion, or interbreeding, not as definitive in itself but as evidence on whether the evolutionary definition is fulfilled. Thus the species as actually used by many progressive systematists in both animals and plants does tend to approximate a unitary phyletic lineage of

separate evolutionary role even though in both cases outbreeding, hybridization, may occur and in some groups of plants this is widespread and usual. Emphasis on unitary evolutionary role may even resolve the theoretical difficulty of defining species in asexually reproducing groups.

This redefinition, or shift of emphasis, or revealing of the implicit basis of much modern evolutionary taxonomy, introduces the element of time into the concept of species, even in the so-called non-dimensional situation. It designates the species, including the "non-dimensional" species, as a unit which has been evolving separately, or which will do so, or, as a rule, both. Decision that populations will evolve separately involves prediction. Such points as wide geographical discontinuity (especially with a strong intervening barrier), morphological divergence, sympatric occurrence without interbreeding, and intersterility are clearly items of evidence for this sort of prediction. Their bearing seems to me more meaningful in evolutionary terms than in the definition of actually or potentially interbreeding populations, although of course the evolutionary species usually is also such a group. The special importance of intersterility, even though no modern taxonomist makes it an absolute requirement for specific separation, is, for instance, evident in this context: intersterility makes the prediction of separate evolutionary roles certain.

The Species in Paleontology: Data and Discontinuities

Part of the endless discussion on species concepts is concerned with the relationship between neontological and paleontological species. Opinions vary from the view that the two usually are quite different (e.g. Elias, 1950) to the view that they are usually essentially the same or that one is only an extension of the other concept (e.g. Mayr, 1950). Both views are correct in the sense that species just like those (by any definition) of neontology do occur in paleontology, but that actual practice regarding them may be more difficult or, at least, necessarily somewhat different in paleontology and that there also occur in paleontology taxonomic groups to which no strictly neontological species concept can properly be applied.

That paleontological data and materials are different from neontological is well known and sometimes overstressed. Direct genetical methods are unavailable in paleontology, but they are very rarely used in neontological taxonomy. The paleontologist usually has parts, only, of the organisms concerned, but the neontologist commonly uses parts, only, of recent organisms. Different parts may be available or used in the two cases, but inferences from them regarding populations may nevertheless be closely analogous or actually identical. Nearly or exactly the same general sorts of data, morphological, distributional, and associational, are frequently used in the practice of paleontological and neontological taxonomy. (Fuller discussion of these points was given in Simpson, 1943.)

The "non-dimensional" species is encountered more frequently in paleontology than in neontology, in spite of the fact that paleontology is inherently more multidimensional than neontology. The neontologist is seldom forced to confine himself to collections from one locality, and is never justified in doing so unless forced. Much paleontological taxonomy is necessarily and properly based on quarry collections or mass collections from one local stratum, associations without appreciable dispersion in space or time and ideally non-dimensional. In such cases neontological concepts and definitions of genetical and evolutionary species apply without modification. (Even Elias, 1950, outspoken opponent of the current rapprochement of neontological with paleontological systematics and of both with genetics, admits that in such cases paleontologists "may be obliged to resort to

neontological concepts of taxonomic terms.")

Discontinuities are more frequent and of more varied sorts in paleontology than in neontology. This has certain disadvantages for paleontological theory and interpretation, but it also has some practical advantages. Discontinuities of observation, only, due to inadequate sampling of local populations or inadequate distribution of sampling stations, occur in both fields but are generally harder to fill in when paleontological. Discontinuities of record, that is, in the organisms actually present and available for sampling in the field, are a particular paleontological problem and may concern both time and space. When samples have been obtained from different localities or horizons, rocks and fossils intermediate between them may not exist. Such discontinuities are, as of now, facts in nature. Their use to delimit taxonomic groups is non-arbitrary, by definition. Yet they do not necessarily coincide with any particular sort of discontinuity that existed when the organisms were alive. Hence their relationship to the sorts of units defined in neontology may be and remain ambiguous.

The special questions involved in succession or sequence will be discussed separately, but it should be noted here that paleontological samples discontinuous in space are often also discontinuous in time and that the possibility can seldom be discarded. With such samples of similar organisms it is always difficult and it may be quite impossible to determine whether:

(a) They represent local populations that were genetically continuous, and hence infraspecific groups by genetical and evolutionary definition.

(b) They represent separate phyletic lineages, and hence distinct genetical and evolutionary species.

(c) They represent ancestral and descendent populations, and hence a special and peculiarly paleontological situation discussed below.

In such a case, the preferred practical procedure is:

1. To consider the two (or more) lots of associated specimens as samples of different local populations and to derive from them estimates of morphological variation in those populations.
2. If the population estimates indicate no significant mean difference, to consider the samples as representative of essentially a single population and hence taxonomic group.
3. If the population estimates indicate significant mean difference but overlap in range of variation, to consider the samples as drawn from different subspecies of one species.
4. If the population estimates indicate no overlap in range of variation (for at least one well-defined character), to consider the samples as drawn from different species.

Species recognized in this way are non-arbitrary in exclusion and inclusion by combined morphological and distributional criteria. They are morphologically similar to most genetical and evolutionary species. In many cases they will in fact be genetical or evolutionary species, but under the stated conditions it is virtually impossible to determine this equivalence with any high degree of probability.

The Species in Paleontology: Succession

Succession on a small scale and involving short periods of time occurs in some neontological data and there involves some special taxonomic problems, but on the whole succession is distinctively paleontological.

Discontinuities of observation and of record are frequent in paleontological study of successive populations. They frequently correspond with discontinuities of time, already mentioned. Diastems, geologically brief intervals of non-deposition (with or without erosion), are abun-

dant in most stratigraphic sequences. They represent local discontinuities in time, but may be considered taxonomically unimportant if there was no significant change in the populations being studied or if intervening fossils of the same or closely similar populations are available from other localities. Larger and regional stratigraphic unconformities are also, although less, common and they usually represent taxonomically significant discontinuities in time.

Discontinuities in succession may also be caused by migration, by change of (biotic, and commonly of correlated stratigraphic) facies, or, frequently, by a combination of both (see especially Bell, 1950, also Newell, 1948). Such discontinuities often coincide with discontinuities in time but, as Bell has stressed, they need not do so. For instance figure 1 shows diagrammatically a situation in which there is a discontinuity of facies, with fossil populations as limited by facies successive wherever found, but really contemporaneous and without discontinuity (or, indeed, regional succession) in time.

When discontinuities in succession are present in the data, they may be dealt with in practice as outlined above for paleontological discontinuities in general. They may similarly permit non-arbitrary delimitation of morphological-distributional species which may approximate, but cannot usually be clearly equated with, genetical-evolutionary species. This greatly simplifies paleontological procedures and in many particular cases it averts the special taxonomic problems inherent in continuity of succession.

Essential continuity in sequences long enough to involve significant progression or diversification of populations is far from universal in paleontology. It is, however, frequent and becomes steadily more so as collecting becomes more extensive. The special problems involved therefore do have great and increasing practical importance. They are of supreme importance for paleontological taxonomic theory. No one seriously doubts that the whole of life has factually been a continuum of populations when the whole sequence is considered, in spite of the innumerable discontinuities in the record.

The genetical-evolutionary concept of species is applicable as between different phyletic branches, evolving lineages, especially if they are contemporary but also if they are not. Thus in figure 2A, *a*, *b*, and *c* are three different species, by genetical or, more clearly, by evolutionary definitions, although *a* and *b* are contem-

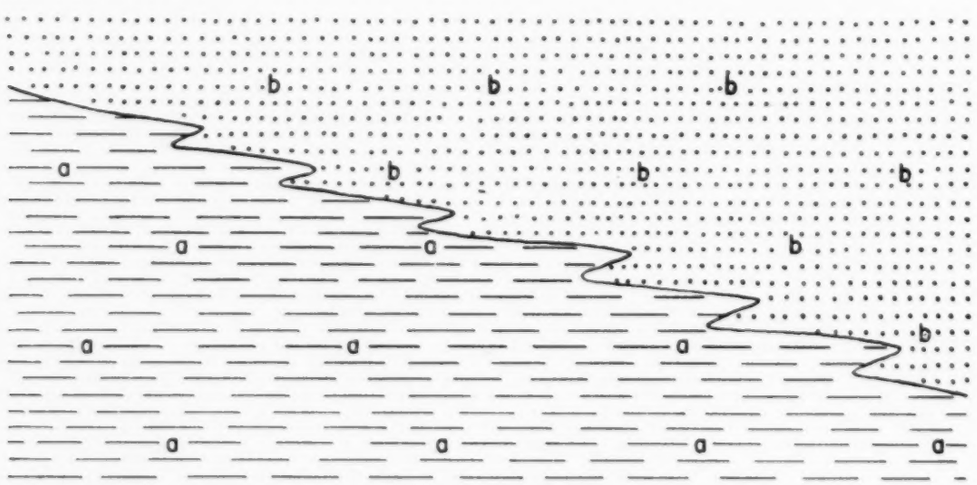

FIG. 1. Diagram of change of facies and fossil succession. Broken lines and dots represent two different rock facies each with a characteristic fossil, *a* and *b*. Although *b* everywhere occurs above *a* in any given local section, the two are, in fact, contemporaneous.

porary with each other but not with *c*. Serious problems in theory, and usually also in practice, arise rather regarding the parts of such a pattern that cannot be distinguished as separate branches.

One possible solution, diagrammed in figure 2B, is to recognize central lines as species and to distinguish branches as other species. This procedure is "correct" from an evolutionary point of view, or, better, the species so designated do fulfill the proposed evolutionary definition even though their delimitation is genetically arbitrary at the points of branching. For rather small groups under exceptionally favorable circumstances the procedure is also practicable and is actually used. Its practicability depends, however, on recognition of an essentially unchanging central line, *a*, and main branches, *b* and *c*. It is, however, more usual even within rather small groups and universal within really large groups and long sequences for all lines to evolve materially. Then it is not practical taxonomy to designate the whole of any one line as a single species, and there is no meaningful criterion for designating "main" or "central" lines and branches. Thus the four alternatives of figure 2C are all equally acceptable interpretations of the same phyletic facts as in figure 2A, in terms of main lines and branches, if all lines are undergoing progressive change. The only reasonable criterion of choice would be designation of certain terminal branches as more important, or somehow definitive, than others. A logical extreme would be, for instance, to take *Homo sapiens* as the supreme species and to consider its ancestry, from the beginning of life (or even before) as the main line, not specifically separable from *H. sapiens*. This arrangement has in fact been seriously proposed by a philosopher (Miller, 1949). Taxonomists will surely agree that this result and the whole procedure involved are impractical if not absurd.

Another possible approach is to recognize each evolutionary lineage as a unitary species until it divides and then to consider the descendent branches as species distinct from each other and from the single ancestral line, as diagrammed in figure 2D. This grouping meets an evolutionary definition of species, although delimitations between adjacent species are arbitrary by genetical criteria. It is, however, both undesirable and impractical. It frequently happens that a population undergoes no essential change even though a branch, a separate species, has arisen from a part of it. E.g. in figure 2D, *d* and *e* may be genetically and morphologically identical in all essentials. It is then not meaningful taxonomy to designate them as separate species. An even more serious objection is practical: the pattern of branching in a paleontological sequence is gradually discovered, perhaps never fully known, and generally depends as much on opinion as on unequivocal data. The taxonomy of long-known species would be changed every time a new branch was discovered or inferred and would be excessively and unnecessarily subject to personal disagreement. Moreover, a phyletic line may change radically between branches (say within *e* of figure 2D), and it is then not useful taxonomy to classify it as the same thing throughout.

The difficulties involved here are merely obscured by the presence of phyletic branching. They arise, regardless of whether or not branching occurs, from the problem of classifying ancestral and descendent stages in a continuously evolving population. Such a population may be diagrammatically represented, as in figure 3A, by a curve of variation (both genetical and morphological), moving through time and also being displaced as its genetical and morphological characters change. A cross-section represents the population at a particular instant in time, as it would be represented by a fossil sample from a single horizon. Such a cross-section is a genetical non-dimensional species, as seen both in neontology and in paleontology.

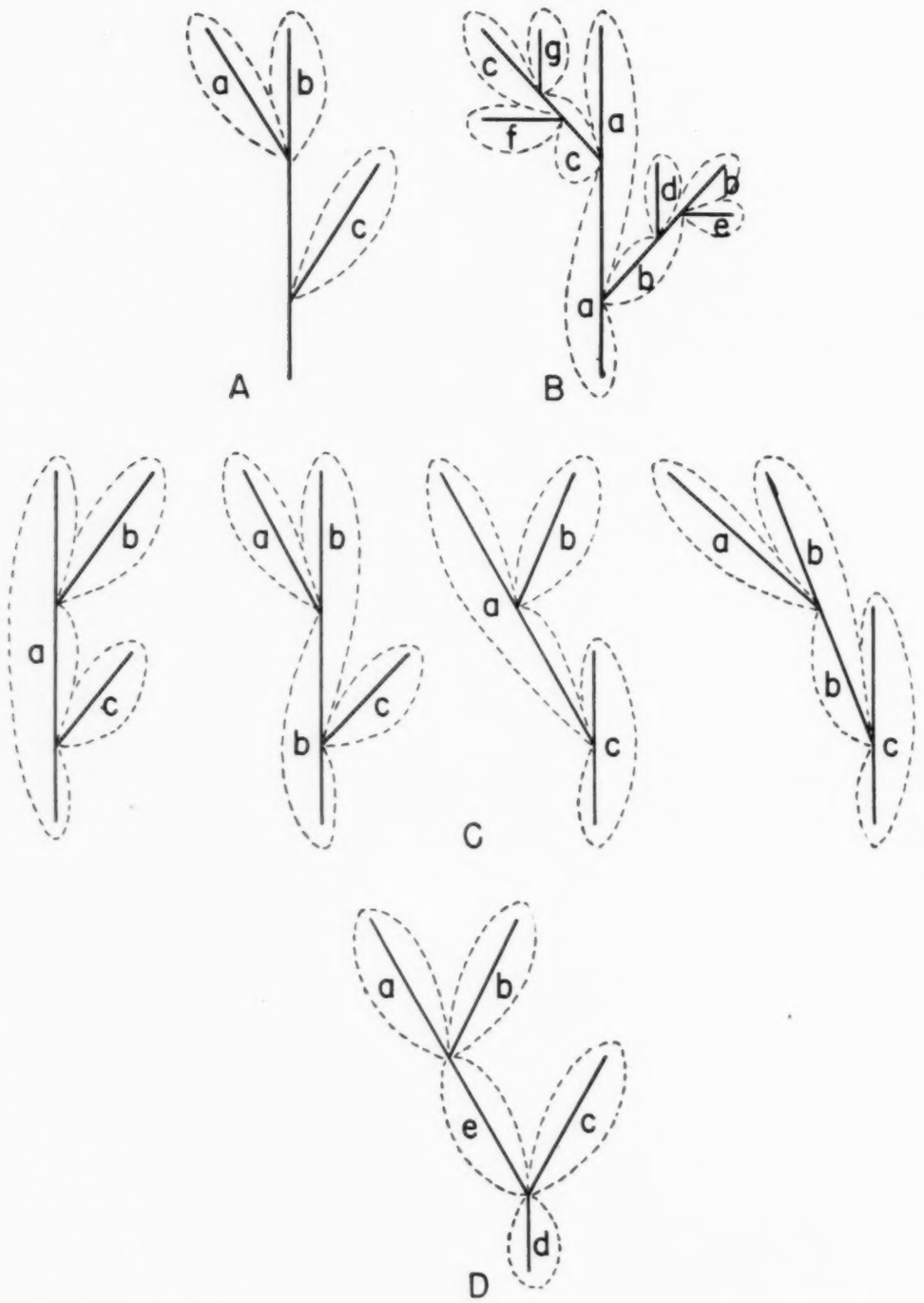

FIG. 2. Classification of successive populations with phyletic sequence and branching. In each diagram, the time sequence is from bottom to top and the solid lines represent phyletic descent. The broken lines enclose phyletic segments classified by various methods as distinct species. A, branching phyletic sequence with three clearly distinct evolutionary species, *a–c*. B, similar but more branched sequence with main lines and branches classified as species. C, four different possibilities of designating main lines and branches in the same phyletic sequence as in A. D, sequence as in A, with species boundaries set at points of branching. See discussion in text.

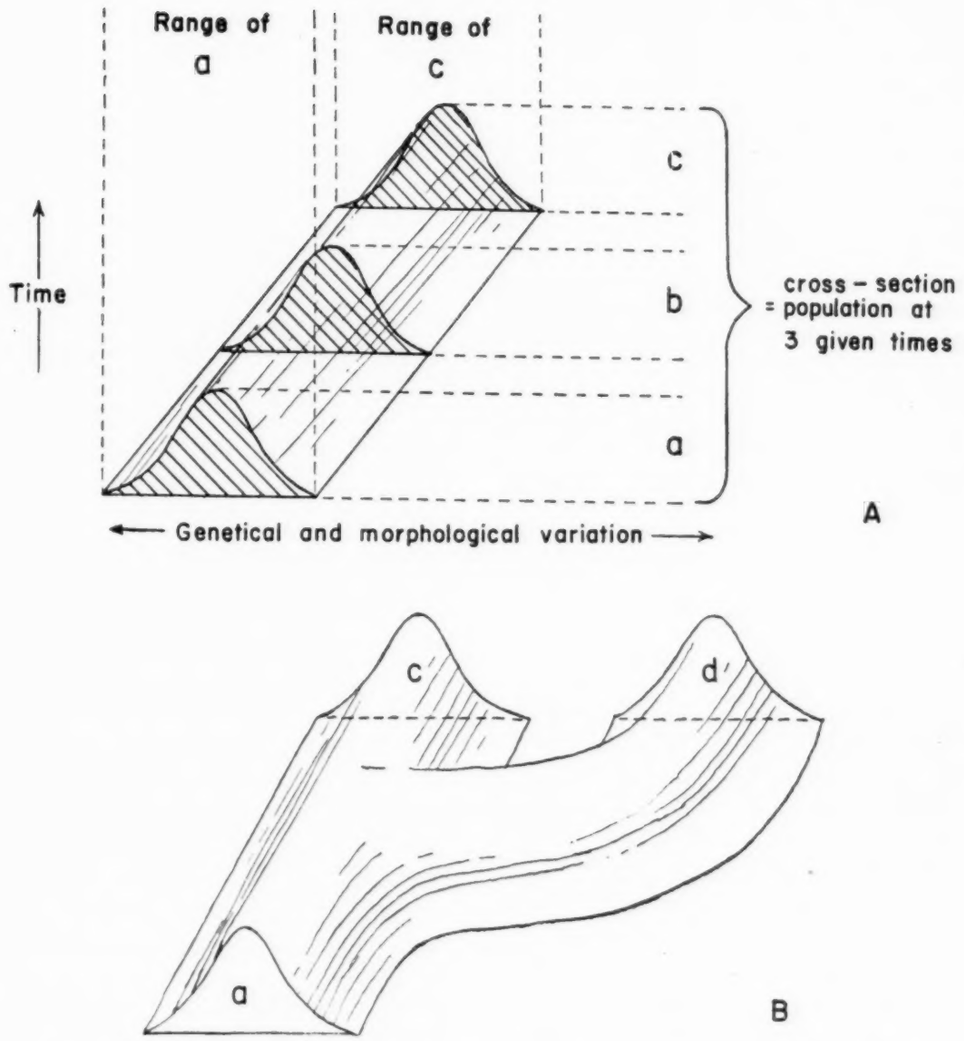

FIG. 3. Phyletic evolution and classification of successive populations. Phyletic sequence in a varying population is represented by a normal curve moving through time and changing in mean character, and by the solid generated thereby. A, sequence without branching. B, branched sequence. See discussion in text.

The whole sequence of populations, *a* to *c* in figure 3A, is genetically continuous and it fulfills the conditions of both genetical and evolutionary definitions of a species, as previously discussed. By these concepts, it is a single taxonomic group, defined as a species. Yet with the passage of time and continuation of progressive evolution, *c* has become quite different from *a*. For purposes of evolutionary study and of practical application to stratigraphy, it is essential that a distinction be made between these populations, which are different.

In practice, the paleontologist calls *a* and *c* different species if, as in figure 3A, the inferred ranges of variation do not overlap. They are *not* different species by the widely accepted genetical criteria or by the proposed evolutionary criteria discussed above. The comparison is clarified in figure 3B in which speciation (in the neontological sense) is represented as also having occurred. In this diagram, *c* and *d* are different species by any current usage; explicitly they are different genetical-evolutionary species and also different species in current paleontological practice.

But *a* and *c* are parts of a single genetical-evolutionary species, although called different species in paleontological practice. The paleontologist thus uses the designation "species" for two sorts of entities which are radically and fundamentally incongruent. The only way in which the species category might be defined so as apparently to include both sorts of entities would be to abandon any evolutionary significance for taxonomy and to use purely morphological criteria. But this is not a useful solution. The general undesirability and impracticality of *purely* morphological taxonomic concepts have been sufficiently emphasized above. Moreover, the *whole* sequence of organisms represented in figure 3B cannot be classified at all, in morphological or any other terms, if the pattern in time, i.e. the evolutionary situation, is ignored. As static, separate pictures, the morphological difference between *a* and *c* and that between *c* and *d* are of the same sort, but within the pattern of the whole group in time, even the morphological relationships are not the same in the two cases, for *a* and *c* are morphologically (as well as genetically) continuous through intervening populations and *c* and *d* are not. (One might say here, in line with Dunbar, 1950, that *c* and *d* are continuous through the sequence *c–a–d*, but the fact that this involves a reversal in direction of time still makes an essential difference from the sequence *a–c* or *c–a*, which is consistent in the direction of time.)

In the situation represented in figure 3A, the desirable and indeed necessary taxonomic separation of *a* and *c*, whether they are called species or by some other category term, is arbitrary, because through intervening stages they are continuous by all meaningful criteria. The placing of an intermediate population, such as *b*, in one category or the other is, of course, also arbitrary. When the data really reflect the continuity of the sequence, intermediate populations must often be placed by rule of thumb rather than by any more positive and meaningful criterion. It is in such situations that the frequent occurrence of discontinuities of record, the absence of part of the sequence *a–c*, is practically useful in providing a means of separating *a* and *c*. This is still a separation in what *was* a continuum, but it is non-arbitrary (by the special definition of that word in this paper) as regards the actually available materials being classified.

Since paleontologists are applying the designation "species" to two fundamentally dissimilar sorts of taxonomic categories, it would appear logical that they confine that name to one of them and use a different name for the other. This has also been suggested, but it runs up against another serious practical difficulty: the paleontologist often does not know and has no way to determine which of the two basically different sorts of groups called "species" he has before him.

It is a common situation to have two discontinuous paleontological samples such as *a* and *c* of figure 4A. (It has been noted that if *a* and *c* are discontinuous in space, the possibility that they are also different in time can seldom be ruled out.) By applying the practical methods previously summarized, the paleontologist can readily draw population inferences from these samples, find that variation probably did not overlap in the populations, and define them as different "species." However, he does not know in what sense they are different species, because he does not know whether the relationship is as in figure 4B or as in figure 4C, and unless other crucial populations can be sampled he may have no conclusive way of finding out. In dealing with different samples from closely similar populations, this is one of the commonest situations in the practice of paleontology.

In such cases, a distinction cannot be made in practice between "species" in the basic genetical or evolutionary sense and in the sense of subdivisions in a continuous ancestral-descendent line. I do not

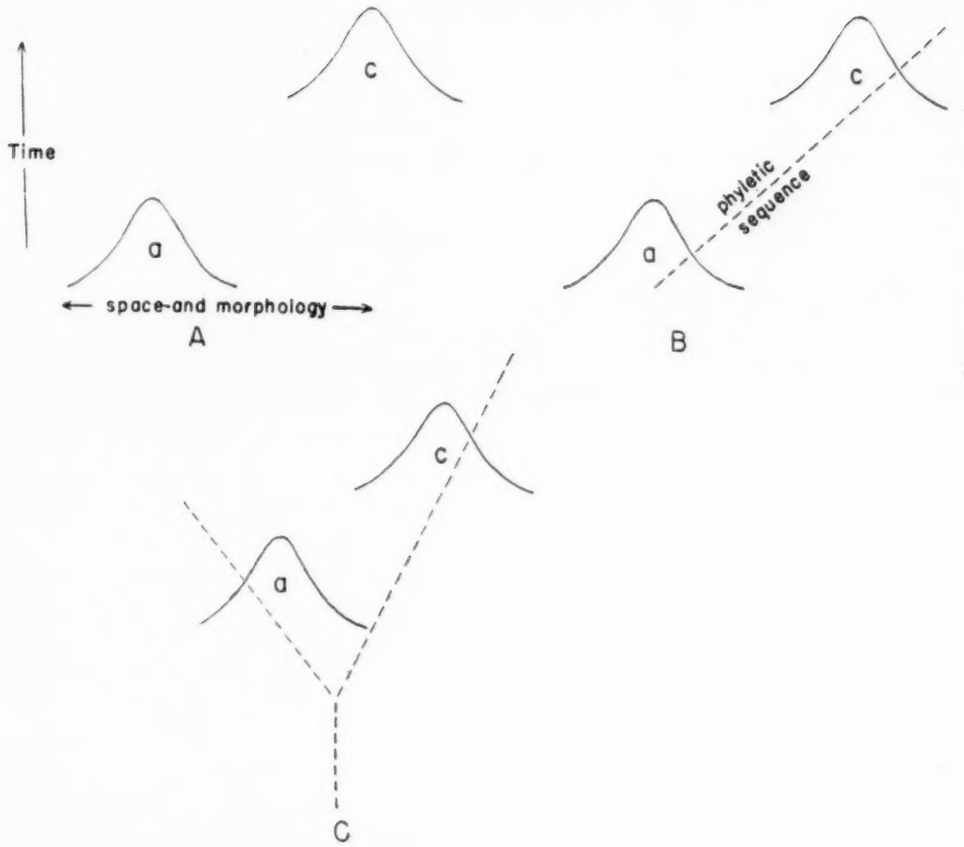

FIG. 4. Diagram illustrating problems of interpretation of two samples of related fossil organisms separated in space and (or, and possibly) in time. The variable populations represented by the samples are represented by normal curves. A, the given situation. B, interpretation as a single phyletic sequence, in which *a* and *c* represent the same species by genetic definition. C, interpretation as a branching sequence, in which *a* and *c* are different species by genetic or evolutionary definition. See discussion in text.

here favor or propose a special term for the latter sort of taxonomic group. I do maintain that it is desirable and useful to realize that these are two quite different things, and that the "species" of paleontological taxonomy may be of either sort.

There are many other pertinent and interesting points that might be considered, such as the problem of dual, partly coincident evolutionary species *a–c* and *a–d* in figure 3B, the uses of evolutionary acceleration and appearance of key characters for separating ancestral and descendent species, or the relationships of subdivisions of choroclines and chronoclines. This paper is, however, sufficiently long already, and the possible extension of its general point of view and method of approach to other points will probably be evident to most taxonomists.

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NATURAL SELECTION AND THE DIFFERENTIATION OF ANGIOSPERM FAMILIES

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Introduction

One of the most striking impressions which results from a comparison between the major subdivisions—families, orders, and classes—of the animal kingdom and the corresponding ones in the higher plants, is that while in animals the characters on which these subdivisions are based are for the most part of obvious adaptive significance, and must have evolved through the guidance of natural selection, in plants this is by no means the case. The different orders of mammals, for instance, either occupy different habitats, such as the Chiroptera and Cetacea, or exploit their habitats in obviously different ways, such as the Carnivora, Perissodactyla, Artiodactyla, Rodentia, etc. The orders of angiosperms, on the other hand, all occupy about the same range of habitats, and most of them have about the same range of types as to gross outward appearance. Although some orders are primarily woody and others mostly herbaceous, many orders, families, and even genera exist which contain the entire range of types from small annuals to good sized trees. Furthermore, most orders and families of angiosperms are essentially similar in their methods of securing food through photosynthesis and absorption of minerals from the soil, as well as in methods of protection from drought, disease, or pests. Whatever specializations exist in these respects are for the most part characteristic of genera, species, or even subspecies (ecotypes), rather than of whole families or orders.

Since the characteristics which differentiate the orders and families of angiosperms are largely confined to the flowers and fruits, their adaptive significance, if present, would of necessity be concerned with different ways of carrying out the two most vital functions connected with the reproduction of the higher plants, namely the transfer of pollen from one plant to another, and the dissemination of seeds. At first sight, the different ways in which plants have solved these problems seem to bear no close relationship to their segregation into orders and families. From the Ranunculaceae to the Labiatae and Compositae species can be found which are pollinated by bees, while pollination by flies, birds, wind, and water is likewise scattered through the angiosperms, with little relationship to the boundaries of the higher categories. The same is true of the different methods of seed dispersal; by wind, water, or animals.

This has led many botanists to belittle or even to deny the role of selection in the origin of the orders and families of angiosperms; one elementary textbook of botany states specifically that differences in the number and arrangement of floral parts cannot possibly affect the survival of the species, and therefore cannot have been brought about by natural selection. This assumption, however, is contrary to those made by students of most other groups of organisms, and if true, would make the evolution of the flowering plants a very anomalous series of processes. Furthermore, there are certain trends in floral evolution which are repeated many times in groups with very diverse affinities. These trends are truly progressive, with so many intermediate conditions found among living species that they cannot have arisen through the occurrence

and establishment of single mutations with large effects on the phenotype. Examples are the trend from many to few or one ovule per carpel, found in the Ranunculaceae, Rosaceae, Malvaceae, and several other groups; and that from superior to inferior ovary, found in the Saxifragaceae, Ericaceae, Rubiaceae, Amaryllidaceae, and elsewhere. That such trends could have taken place through a progressive series of mutations, occurring either by chance or through some internally directed, "orthogenetic" tendency without the aid of selection, seems as improbable in these plants as in other organisms.

Nevertheless, the presence as common, flourishing organisms of plants representing both the "primitive" and the "advanced" stages of these phylogenetic trends makes impossible the assumption that either condition is by itself intrinsically better than the other. In eastern North America, the most abundant, diversified, and successful members of the Ericales are the Vacciniaceae, which have the ovary inferior, while in Europe and Africa the most successful members of the order are the tribe Ericoideae of the Ericaceae, in which the ovary is superior. In the Raunculaceae, the genera *Ranunculus, Anemone, Clematis,* and *Thalictrum,* all of which have the number of seeds per carpel reduced to one, are among the most successful genera of their family, but *Caltha, Delphinium, Aconitum,* and *Aquilegia,* which have the presumably primitive condition of numerous seeds per carpel, are almost equally successful.

We cannot assume, therefore, that these trends have occurred because the advanced condition has by itself had a selective advantage over the original one. But this does not preclude the hypothesis that these trends have been guided by natural selection. We must remember that adaptiveness and selective value are for the most part characteristic not of individual characters, but of entire organs. The flower and fruit are structures which perform two essential functions for the plant; first the transfer of pollen from one individual of a species to another, with prevention or restriction of pollination between individuals belonging to different species; and second the formation and dissemination of a type of seed which is able to germinate and produce a vigorous seedling in the habitat to which the adult plant is adapted. On this basis, the adaptive significance of the differences in floral structure between families of angiosperms must be considered in terms of character combinations, rather than single characters.

The writer has therefore set up the following working hypothesis: the combinations of characteristics found in the larger, more successful families of flowering plants evolved and became established through the guidance of natural selection because they represented particularly successful methods of solving the problems of fertilization, seed dispersal, or both under the conditions of habitat and the type of vegetative growth which existed in the ancestors of these families at the time when they originated. This hypothesis could be tested in three ways: first through comparative studies of closely related species which show recognizable trends in specialization of their reproductive structures, second through studies of the action of certain particular selective agents in producing a diversity of genera and species, and third through a survey of the combinations of reproductive characteristics found in the angiosperms as a whole.

The first type of evidence can best be obtained by monographers of genera or families, but comparatively few such workers have paid attention to the possible adaptive significance of the differences which they have recorded. Three recent exceptions are Babcock's (1947) monograph of *Crepis,* Li's (1948, 1951) of *Pedicularis,* and Pennell's (1948) discussion of the Scrophulariaceae. Although none of these studies provide as complete data on adaptiveness as one might desire,

they nevertheless give an idea of what can be learned when a group is studied carefully with this end in view. In *Crepis,* Babcock noted that the rhizomatous perennials which are very long lived and grow mostly in the relatively stable habitats of forests and swamps, have large, relatively unspecialized involucres and achenes. The tap-rooted perennials, which may or may not be very long lived, and which often grow in relatively impermanent, "pioneer" habitats, are intermediate in the size and specialization of their involucres and achenes. Finally the annual species have highly specialized involucres with much thickened inner bracts, and predominantly small, often long-beaked achenes, very well adapted for wide dispersal of the seeds. In the nearly two hundred species of this genus, these correlated trends of shortening the life cycle and increasing the specialization of the reproductive parts have taken place independently in several different lines of evolution, and they are the basis of the differentiation of sections within the genus.

In *Pedicularis,* the differentiation of the species has been based chiefly on the differentiation of the corolla, stamens, and style, forming different adaptations to cross pollination by insects. One whole group of species, found in the mountains of Asia, differs from the rest of the genus in the very long corolla tube. These species are pollinated by Lepidoptera, while the remaining ones are pollinated mostly by bees.

The adaptation of floral structures to cross pollination by insects has been studied by many workers since the time of Darwin. Grant's (1949) recent summary of this subject has brought out clearly the degree to which pollination by specialized insects has promoted differentiation between species and genera in respect to those parts of the flower concerned with cross pollination. While the differences tabulated by him, like those studied by Babcock, Li, Pennell, and other monographers, are those distinguishing species and genera rather than families, there is no reason to believe that family and order differences arose in a different way. As will be emphasized later in this discussion, all of the character differences used by systematists to separate families and orders can be found in some families as differences between genera of the same family, or even sections or subgenera of the same genus. There is good reason to believe, therefore, that in the remote period of geologic time, probably the Cretaceous period, when the ancestors of the modern families became differentiated from each other, their interrelationships were much like those between modern species and genera, and were governed by similar selective factors.

In a later and even more stimulating paper, Grant (1950) has suggested a specific selective value for epigyny, namely the protection of the flower from biting insects and birds. This ingenious hypothesis will be discussed later.

Method of Analysis

The third type of approach, the survey of the combinations of reproductive characteristics found in angiosperms as a whole, is the one adopted in this study. The survey was conducted as follows. Eight diagnostic characters were selected because they are the ones most frequently used in both manuals of regional floras and general works like Engler and Prantl's "Die Natürlichen Pflanzenfamilien" and Hutchinson's "Families of Flowering Plants."

For each character two conditions were recognized, one considered by many or all systematists as primitive and the other as advanced. The characters and their alternative conditions are given in table 1. The writer recognizes that this system involves a certain amount of artificiality. In the first place, the assumption of one condition as primitive and the other as advanced may not always be correct. The absence of petals, the union of petals and sepals, the union of carpels (as compared to apocarpy), the reduction of

seeds to one per carpel, and the inferior ovary, are all frequently recognized as advanced conditions with respect to those characters, although they may exist in groups which are otherwise regarded as primitive. This statement, which is in contrast to the basic assumption made by Sporne (1948, 1949) in his recent attempt to determine the nature of the primitive flower, will be discussed more fully, in connection with Sporne's work, after the writer has presented his own evidence.

On the other hand, occasional reversals of some evolutionary tendencies may occur. Examples of this nature will be presented later in the discussion. Since, however, the object of the present study is to determine the possible adaptive significance of similar character combinations, whatever their origin, the occasional errors which may have been introduced by such misjudgments of phylogeny would not distort very much the evidence pertaining to adaptation.

More serious is the distortion produced by the recognition of only two conditions in respect to each character. This was necessary because of the great complexity which would have resulted if more conditions had been recognized. The division into categories was carried out for certain characters as follows. In respect to character 1, all acyclic or spirally arranged perianths were classified with the dichlamydous types, since they are certainly primitive. Types without petals were considered as monochlamydous, even though the sepals were enlarged and petal-like. In respect to sympetaly (character 2), groups possessing both calyx and corolla were classified as sympetalous only if both calyx and corolla had their parts united, but monochlamydous groups, with the petals absent, were placed in the advanced "sympetalous" classification if their sepals were united. In respect to character 3, flowers were considered zygomorphic primarily on the basis of their corollas, but in some groups, particularly those related to clearly zygomorphic forms, zygomorphy was recorded chiefly on the basis of stamens, particularly if the number of stamens was fewer than that of corolla lobes. In respect to placentation (character 7), the condition was recorded as axial if the edges of each carpel were united or closely oppressed to each other, so that each functional carpel formed a separate loculus of the ovary. This resulted in classifying the apparently basal placentation of some

TABLE 1. *List of the eight characters used most frequently in the classification of the families of angiosperms*

Character		Number in Chart
Primitive	Advanced	
Calyx and corolla both present (dichlamydous).	Corolla or entire perianth absent (mono- or achlamydous).	1
Petals separate (polypetalous).	Petals (sepals in monochlamydous forms) united (sympetalous).	2
Calyx and corolla regular (actinomorphic).	Perianth irregular (zygomorphic).	3
Stamens more numerous than perianth members (polystemonous).	Stamens the same number as or fewer than perianth members (oligostemonous).	4
Carpels separate (apocarpous).	Carpels united (syncarpous).	5
Seeds more than one per carpel (many).	Seeds not more than one per carpel (few).	6
Placentation axial.	Placentation parietal, basal, or free central.	7
Carpels not united with the receptacle or perianth (hypogyny or perigyny).	Carpels united with receptacle, perianth, or both (epigyny).	8

TABLE 2. *List of families and part families, arranged according to presumable primitive or advanced condition in respect to the eight characters listed in table 1*

Primitive in all characters (0). 6 whole, 6 part families.

*w Magnoliaceae (part)
w Winteraceae
w Schisandraceae
w Degeneriaceae
w Anonaceae (part)
h Ranunculaceae (part)
w Lardizabalaceae
w Dilleniaceae
w Crossosomataceae
w Cunoniaceae (part)
w Rosaceae (part)
w Mimosaceae (part)

Zygomorphic, otherwise primitive (3). 1 part family.

h Ranunculaceae (part)

Oligostemonous, otherwise primitive (4). 5 part families.

h Crassulaceae (part)
h Saxifragaceae (part)
w Ochnaceae (part)
w Mimosaceae (part)
w Caesalpiniaceae (part)

Ovules few, otherwise primitive (6). 3 whole, 6 part families.

w Magnoliaceae (part)
w Himantandraceae
w Menispermaceae (part)
h Ranunculaceae (part)
w Ochnaceae (part)
w Cunoniaceae (part)
wh Rosaceae (part)
w Calycanthaceae
m Alismaceae

Placentation parietal, otherwise primitive (7). 1 part family.

m Butomaceae (part)

Mono- or achlamydous, otherwise primitive (1). 2 families.

w Trochodendraceae
w Cercidiphyllaceae

Syncarpous, otherwise primitive (5). 12 whole, 8 part families.

w Anonaceae (part)
h Ranunculaceae (Nigella)
h Nympheaceae
wh Capparidaceae (part)
h Papaveraceae (most)
h Sarraceniaceae
w Sonneratiaceae
w Theaceae
w Medusagynaceae
w Actinidiaceae
w Ochnaceae (part)
w Chlaenaceae
wh Hypericaceae (part)
w Eucryphiaceae
w Scytopetalaceae (part)
w Tiliaceae (part)
w Gonostylaceae
w Bombacaceae
wh Malvaceae (part)
w Hydrangeaceae (Carpenteria)

Sympetalous, otherwise primitive (2). 1 part family.

w Mimosaceae (part)

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* w = woody; wh = containing both woody and herbaceous species; h = herbaceous; m = monocotyledon.

Families spaced close together belong in the same order; those separated by wider spaces belong to different orders.

TABLE 2.—*Continued*

Oligostemonous, seeds few (46). 4 whole, 4 part families.

w Lauraceae
wh Berberidaceae
w Menispermaceae (part)
w Ochnaceae (part)
w Cunoniaceae (part)
wh Rosaceae (part)
w Connaraceae
m Triuridaceae

Oligostemonous, parietal placentation (47). 1 part family.

m Butomaceae (part)

Monochlamydous, oligostemonous (14). 1 family.

w Lactoridaceae

Zygomorphic, syncarpous (35). 1 part family.

wh Capparidaceae (part)

Oligostemonous, syncarpous (45). 9 whole, 11 part families.

wh Capparidaceae (part)
h Cruciferae (most)
h Saxifragaceae (part)
wh Lythraceae
h Tovariaceae
h Elatinaceae
h Oxalidaceae
h Byblidaceae
w Ochnaceae (part)
w Cunoniaceae (part)
w Hippocrateaceae
w Rutaceae (part)
w Meliaceae (part)
w Melianthaceae (part)
w Staphyleaceae
w Clethraceae
wh Ericaceae (part)
h Monotropaceae (part)
m Liliaceae (part)
m Philesiaceae (part)

Syncarpous, ovules few (56). 4 whole, 6 part families.

w Caryocaraceae
w Ochnaceae (part)
w Dipterocarpaceae
w Quiinaceae
w Tiliaceae (part)
w Scytopetalaceae (part)
wh Malvaceae (part)
w Humiriaceae
w Cunoniaceae (part)
w Hydrangeaceae (Whipplea)

Syncarpous, parietal, etc., placentation (57). 2 whole, 7 part families.

h Papaveraceae (Argemone)
h Capparidaceae (Polanisia)
h Portulacaceae (part)
w Bixaceae (part)
w Cochlospermaceae
w Flacourtiaceae (part)
w Canellaceae (most)
w Marcgraviaceae
w Hypericaceae (part)

Monochlamydous, syncarpous (15). 1 family.

h Nepenthaceae

Sympetalous, oligostemonous (24). 1 whole, 3 part families.

h Crassulaceae (part)
w Mimosaceae (Schrankia)
wh Apocynaceae (part)
wh Asclepiadaceae

Zygomorphic, oligostemonous (34). 2 part families.

wh Caesalpiniaceae (part)
wh Papilionaceae (most)

TABLE 2.—*Continued*

Syncarpous, epigynous (58). 4 whole, 3 part families.

w Eupomatiaceae
h Aizoaceae (part)
w Myrtaceae
w Lecythidiaceae
w Rhizophoraceae
w Hydrangeaceae (part)
w Rosaceae (part)

Mono- or achlamydous, oligostemonous, seeds few (146). 10 whole families.

w Gomortegaceae
w Myristicaceae
h Cephalotaceae
w Brunelliaceae
w Leitneriaceae
w Platanaceae
m Juncaginaceae
m Najadaceae
m Sparganiaceae
m Typhaceae

Oligostemonous, syncarpous, seeds few (456). 25 whole, 11 part families.

h Koeberliniaceae
h Linaceae
h Limnanthaceae
h Geraniaceae (most)
wh Zygophyllaceae
w Coriariaceae
w Ochnaceae (part)
w Tremandraceae
w Malpighiaceae (part)
w Erythroxylaceae
w Dichapetalaceae
w Hamamelidaceae (part)
w Aquifoliaceae
w Celastraceae
w Cyrillaceae
w Cneoraceae
w Pandaceae
w Salvadoraceae (most)
w Stackhousiaceae
w Olacaceae (part)
w Rhamnaceae
w Vitaceae
wh Rutaceae (most)
w Simarubaceae
w Burseraceae
w Meliaceae (part)
w Sapindaceae (part)
w Akaniaceae
w Aceraceae
w Sabiaceae
w Didieraceae
w Anacardiaceae
m Commelinaceae (part)
m Flagellariaceae
m Rapateaceae
m Liliaceae (part)

Oligostemonous, syncarpous, parietal, etc., placentation (457). 13 whole, 6 part families.

h Turneraceae
wh Capparidaceae (part)
h Saxifragaceae (Parnassia)
h Droseraceae
h Caryophyllaceae
h Portulacaceae (part)
w Pittosporaceae
w Flacourtiaceae (part)
wh Cistaceae
h Frankeniaceae
w Tamaricaceae
wh Malesherbiaceae
h Passifloraceae
h Achariaceae
w Caricaceae
w Myrsinaceae (part)
m Mayacaceae
m Xyridaceae
m Philesiaceae (part)

Monochlamydous, oligostemonous, syncarpous (145). 1 whole, 2 part families.

h Aizoaceae (part)
w Sterculiaceae (part)
w Myrothamnaceae

TABLE 2.—*Continued*

Monochlamydous, syncarpous, seeds few (156). 1 whole, 1 part family.

h Phytolaccaceae
w Hamamelidaceae (Fothergilla)

Monochlamydous, syncarpous, parietal, etc., placentation (157). 1 whole, 2 part families.

w Canellaceae (part)
w Salicaceae (Populus)
m Pandanaceae

Monochlamydous, synsepalous, oligostemonous (124). 1 part family.

w Proteaceae (part)

Zygomorphic, oligostemonous, seeds few (346). 2 part families.

w Caesalpiniaceae (Krameria)
wh Papilionaceae (part)

Sympetalous, oligostemonous, syncarpous (245). 5 whole, 12 part families.

w Meliaceae (part)
w Ericaceae (most)
w Epacridaceae
h Monotropaceae
wh Diapensiaceae
w Styracaceae (part)
wh Loganiaceae
wh Apocynaceae (part)
h Plantaginaceae (part)
h Campanulaceae (part)
wh Polemoniaceae (part)
wh Hydrophyllaceae (part)
wh Solanaceae
m Bromeliaceae (part)
m Liliaceae (part)
m Philesiaceae (part)
m Haemodoraceae (part)

Sympetalous, syncarpous, seeds few (256). 2 whole families.

w Ebenaceae
w Styracaceae (part)

Sympetalous, syncarpous, parietal, etc., placentation (257). 1 whole family.

w Fouquieriaceae

Zygomorphic, oligostemonous, syncarpous (345). 1 whole, 4 part families.

h Cruciferae (Streptanthus)
w Trigoniaceae
h Saxifragaceae (part)
w Melianthaceae (part)
w Vochysiaceae (part)

Zygomorphic, syncarpous, placentation parietal, etc. (357). 1 whole, 2 part families.

wh Capparidaceae (part)
w Bixaceae (part)
h Resedaceae

Oligostemonous, syncarpous, epigynous (458). 2 whole, 8 part families.

h Saxifragaceae (part)
wh Onagraceae (most)
wh Melastomaceae (part)
w Hydrangeaceae (part)
m Alstroemeriaceae (part)
m Amaryllidaceae (part)
m Iridaceae (part)
m Velloziaceae (part)
m Apostasiaceae
m Burmanniaceae

Syncarpous, seeds few, epigynous (568). 1 part family.

w Rosaceae (part).

Syncarpous, parietal, etc., placentation, epigynous (578). 3 whole, 2 part families.

w Punicaceae
h Begoniaceae
wh Loasaceae (part)
h Cactaceae
m Hydrocharitaceae (part)

TABLE 2.—*Continued*

Monochlamydous, syncarpous, epigynous (158). 1 part family.

w Myrtaceae (part)

Oligostemonous, syncarpous, seeds few, placentation basal or apical (4567). 2 whole, 5 part families

wh Capparidaceae (part)
wh Illecebraceae (part)
w Flacourtiaceae (part)
w Corynocarpaceae
w Icacinaceae (part)
w Olacaceae (part)
m Eriocaulaceae

Monochlamydous, oligostemonous, syncarpous, ovules few (1456). 6 whole, 2 part families.

h Callitrichaceae
w Geissolomataceae
w Sterculiaceae (part)
wh Euphorbiaceae
w Buxaceae
w Empetraceae
m Thurniaceae
m Restioniaceae (part)

Mono- or achlamydous, oligostemonous, syncarpous, parietal placentation (1457). 2 whole, 1 part family.

h Saururaceae
w Salicaceae (part)
m Juncaceae

Monochlamydous, synsepalous, oligostemonous, seeds few (1246). 1 part family.

w Proteaceae (part)

Sympetalous, oligostemonous, syncarpous, seeds few (2456). 6 whole, 6 part families.

w Ericaceae (part)
h Lennoaceae
w Sapotaceae
w Styracaceae (part)
w Myrsinaceae (most)
w Diclidantheraceae
w Lissocarpaceae
w Oleaceae
wh Boraginaceae (part)
h Convolvulaceae
h Plantaginaceae
m Liliaceae (part)

Sympetalous, oligostemonous, syncarpous, parietal or free central placentation (2457). 3 whole, 2 part families.

h Gentianaceae
h Primulaceae
w Myrsinaceae (part)
wh Hydrophyllaceae (part)
m Roxburghiaceae

Monochlamydous, synsepalous, stamens few, syncarpous (1245). 1 part family.

h Aizoaceae (part)

Monochlamydous, synsepalous, syncarpous, parietal placentation (1257). 1 whole family, 1 part family.

h Aizoaceae (part)
m Cyclanthaceae

Zygomorphic, oligostemonous, syncarpous, ovules few (3456). 3 whole, 5 part families.

wh Polygalaceae
w Vochysiaceae (part)
h Geraniaceae (part)
h Tropeolaceae
h Balsaminaceae
w Malpighiaceae (part)
w Sapindaceae (most)
m Commelinaceae (part)

Zygomorphic, oligostemonous, syncarpous, parietal placentation (3457). 2 whole, 2 part families.

wh Capparidaceae (part)
h Fumariaceae (most)
wh Violaceae
w Moringaceae

TABLE 2.—*Continued*

Oligostemonous, syncarpous, seeds few, epigynous (4568). 6 whole, 2 part families.

w Oliniaceae
h Onagraceae (part)
w Bruniaceae
wh Cornaceae
wh Araliaceae
h Umbelliferae
m Amaryllidaceae (part)
m Dioscoreaceae

Oligostemonous, syncarpous, parietal placentation, epigynous (4578). 1 whole, 4 part families.

wh Loasaceae (part)
h Saxifragaceae (part)
w Grossulariaceae
m Hydrocharitaceae (part)
m Burmanniaceae (part)

Monochlamydous, synsepalous, zygomorphic, oligostemonous (1234). 1 part family.

w Proteaceae (part)

Sympetalous, zygomorphic, oligostemonous, syncarpous (2345). 1 whole, 3 part families.

w Ericaceae (Rhododendron)
wh Polemoniaceae (part)
wh Scrophulariaceae
h Acanthaceae (part)

Sympetalous, oligostemonous, syncarpous, epigynous (2458). 1 whole, 9 part families.

w Vacciniaceae
wh Rubiaceae (part)
w Caprifoliaceae (part)
h Campanulaceae (most)
m Bromeliaceae (part)
m Amaryllidaceae (part)
m Iridaceae (part)
m Dioscoreaceae (part)
m Haemodoraceae (part)
m Velloziaceae (part)

Sympetalous, syncarpous, ovules few, epigynous (2568). 1 part family.

w Symplocaceae (part)

Monochlamydous, synsepalous, syncarpous, epigynous (1258). 1 part family.

h Aizoaceae (part)

Zygomorphic, oligostemonous, epigynous (3458). 2 whole, 5 part families.

w Melastomaceae (part)
m Alstroemeriaceae (part)
m Amaryllidaceae (part)
m Iridaceae (part)
m Cannaceae
m Phylidraceae (part)
m Orchidaceae

Monochlamydous, oligostemonous, syncarpous, ovules few, placentation basal or apical (14567) 21 whole, 3 part families.

wh Piperaceae
wh Chloranthaceae
w Lacistemaceae
wh Polygonaceae
wh Illecebraceae (part)
wh Chenopodiaceae
wh Amaranthaceae
w Hamamelidaceae (part)
w Eucommiaceae
w Myricaceae
w Balanopsidaceae
w Betulaceae
w Casuarinaceae
w Ulmaceae
w Barbeyaceae
w Moraceae
h Cannabinaceae
h Urticaceae
m Lilaeaceae
m Posidoniaceae
m Araceae
m Palmae
m Restioniaceae (part)
m Cyperaceae

TABLE 2.—*Continued*

Sympetalous, oligostemonous, syncarpous, seeds few, placentation basal or apical (24567). 2 whole, 3 part families.

w Opiliaceae
w Icacinaceae (part)
wh Plumbaginaceae
wh Hydrophyllaceae (part)
h Plantaginaceae (Littorella)

Monochlamydous, synsepalous, oligostemonous, syncarpous, seeds few (12456). 2 whole, 1 part family.

h Aizoaceae (part)
w Batidaceae
w Peneaceae

Monochlamydous, synsepalous, oligostemonous, syncarpous, parietal placentation (12457). 1 part family.

h Aizoaceae (part)

Zygomorphic, oligostemonous, syncarpous, seeds few, placentation basal (34567). 1 whole, 1 part family.

h Fumariaceae (part)
m Gramineae

Monochlamydous, zygomorphic, oligostemonous, syncarpous, seeds few (13456). 1 whole family.

m Centrolepidaceae

Monochlamydous, zygomorphic, oligostemonous, syncarpous, central placentation (13457). 1 whole family.

h Podostemonaceae

Oligostemonous, syncarpous, seeds few, placentation apical, epigynous (45678). 1 whole, 2 part families.

wh Loasaceae (part)
w Combretaceae
w Olacaceae (part)

Monochlamydous, oligostemonous, syncarpous, seeds few, epigynous (14568). 1 whole family.

h Halorrhagidaceae

Monochlamydous, oligostemonous, syncarpous, parietal placentation, epigynous (14578). 1 part family.

m Hydrocharitaceae (part)

Monochlamydous, synsepalous, zygomorphic, oligostemonous, seeds few (12346). 1 part family.

w Proteaceae (part)

Sympetalous, zygomorphic, oligostemonous, syncarpous, seeds few (23456). 5 whole, 3 part families.

wh Boraginaceae (part)
h Acanthaceae (part)
h Globulariaceae
w Myoporaceae
h Selaginaceae
wh Verbenaceae
wh Labiateae
m Pontederiaceae (part)

Sympetalous, zygomorphic, oligostemonous, syncarpous, parietal placentation (23457). 5 whole, 1 part family.

h Orobanchaceae
h Lentibulariaceae
wh Gesneriaceae (part)
wh Bignoniaceae
h Pedaliaceae
m Pontederiaceae (part)

TABLE 2.—*Continued*

Sympetalous, oligostemonous, syncarpous, seeds few, epigynous (24568). 8 part families.

w Vacciniaceae (part)
w Styracaceae (part)
w Symplocaceae (part)
wh Rubiaceae (part)
wh Caprifoliaceae (part)
m Amaryllidaceae (part)
m Dioscoreaceae (part)
m Haemodoraceae (part)

Sympetalous, oligostemonous, syncarpous, parietal or free central placentation, epigynous (24578). 3 whole families.

m Petermanniaceae
m Taccaceae
m Burmanniaceae

Monochlamydous, synsepalous, oligostemonous, syncarpous, epigynous (12458). 1 part family.

h Aristolochiaceae (part)

Monochlamydous, synsepalous, syncarpous, ovules few, placentation axial, epigynous (12568). 1 part family

h Aizoaceae (part)

Monochlamydous, synsepalous, syncarpous, placentation parietal, epigynous (12578). 1 part family.

h Aizoaceae (part).

Zygomorphic, oligostemonous, syncarpous, seeds few, epigynous (34568). 2 part families.

m Iridaceae (part)
m Marantaceae (part)

Zygomorphic, oligostemonous, syncarpous, parietal placentation, epigynous (34578). 1 part family.

m Phylidraceae (part)

Sympetalous, zygomorphic, oligostemonous, syncarpous, epigynous (23458). 5 part families.

w Caprifoliaceae (part)
wh Lobeliaceae (most)
m Iridaceae (Freesia)
m Musaceae (most)
m Zinigiberaceae (most)

Monochlamydous, synsepalous, oligostemonous, syncarpous, seed solitary, placentation basal or apical (124567). 3 whole, 1 part family.

h Aizoaceae (part)
wh Thymeleaceae
wh Nyctaginaceae
h Balanophoraceae

Monochlamydous, oligostemonous, seed solitary, placentation basal or apical, epigynous (145678). 4 whole, 1 part family.

w Loranthaceae (part)
w Grubbiaceae
w Myzodendraceae
w Fagaceae
w Garryaceae

Sympetalous zygomorphic, oligostemonous, syncarpous, seed solitary, placentation basal (234567). 1 whole family.

h Phrymaceae.

Sympetalous, oligostemonous, syncarpous, seed solitary, placentation basal or apical, epigynous (245678). 1 whole, 3 part families.

wh Compositae (part)
h Calyceraceae
w Olacaceae (part)
w Loranthaceae (part)

Monochlamydous, synsepalous, oligostemonous, syncarpous, placentation parietal, epigynous (124578). 3 whole families.

h Cucurbitaceae
h Rafflesiaceae
h Hydnoraceae

TABLE 2.—*Continued*

Zygomorphic, oligostemonous, syncarpous, seed solitary, placentation basal, epigynous (345678). 1 part family.

m Marantaceae (part)

Sympetalous, zygomorphic, oligostemonous, syncarpous, seeds few, epigynous (234568). 1 whole, 2 part families.

h Goodeniaceae
m Musaceae (part)
m Marantaceae (part)

Sympetalous, zygomorphic, oligostemonous, syncarpous, parietal placentation, epigynous (234578). 1 whole, 3 part families.

w Columelliaceae
wh Gesneriaceae (part)
wh Lobeliaceae (part)
m Zingiberaceae (part)

Monochlamydous, synsepalous, zygomorphic, oligostemonous, syncarpous, epigynous (123458). 1 part family.

wh Aristolochiaceae (part)

Monochlamydous, synsepalous, oligostemonous, syncarpous, seeds few, placentation basal or apical, epigynous (1245678). 5 whole, 1 part family.

w Octoknemataceae
w Loranthaceae (part)
w Santalaceae
w Eleagnaceae
w Juglandaceae
w Julianaceae

Sympetalous, zygomorphic, oligostemonous, syncarpous, seeds few, placentation basal or apical, epigynous (2345678). 2 whole, 1 part family.

h Valerianaceae
h Dipsacaceae
wh Compositae (part)

carpels containing a single ovule (e.g. Celastraceae, Euphorbiaceae, Umbelliferae, etc.) as a modified axial type. Free central placentation was considered to be derived from the parietal or basal types, since in all three of these conditions the carpel walls do not form complete septa. Perigyny was classified with hypogyny rather than epigyny because there are fewer transitional conditions between perigynous and epigynous types than between perigynous and hypogynous types.

Table 2 is a list of all of the families of angiosperms classified as to their primitive or advanced condition with respect to the eight characters listed in table 1. The families are recognized for the most part following Hutchinson's (1926, 1934) "Families of Flowering Plants." This work was followed chiefly because many of the larger families recognized by Engler and Prantl and others who follow their system are admittedly artificial groupings. Nevertheless, even the smaller families of Hutchinson frequently show variation in one or more of the eight characters listed, and so had to be listed under several different combinations of characters. Often one or two genera differ from the others of their family in one of these characteristics; several of these genera are placed in parentheses after the name of the family to which they belong. In the more variable families, the descriptions of individual genera were studied in order to make the classification as accurate as possible, but many instances of genera deviating from the rest of their family were doubtless overlooked. Their number, however, can hardly be great enough to affect the general picture presented by the data.

PRESENTATION OF RESULTS

The results given in table 2 are presented diagrammatically in figures 1 and 2. These figures were constructed as follows. The 256 squares of the chart

represent the possible combinations of primitive vs. advanced conditions with respect to the eight characters of table 1. At the head of the horizontal and vertical columns have been placed numbers which refer to the advanced condition in the characters or character combinations which they designate. Each square, therefore, represents the advanced condition with respect to the characters designated by the number appearing at the head of both the horizontal and the vertical columns leading to that square, and the primitive condition with respect to the others. Each square representing a combination realized by one or more groups (families or part families) contains a number indicating the number of groups possessing that combination.

In figure 1, these numbers are presented without further explanation, in order to emphasize their irregular distribution. In figure 2, the same numbers are presented along with a series of explanatory symbols. These are as follows. If one or more groups possessing a particular combination are relatively large, containing twenty or more genera, the number is surrounded by one or more thin circles; except that the presence of five such groups is indicated by a thick circle. The scalloped circular lines indicate very large groups, containing two hundred or more genera. The various

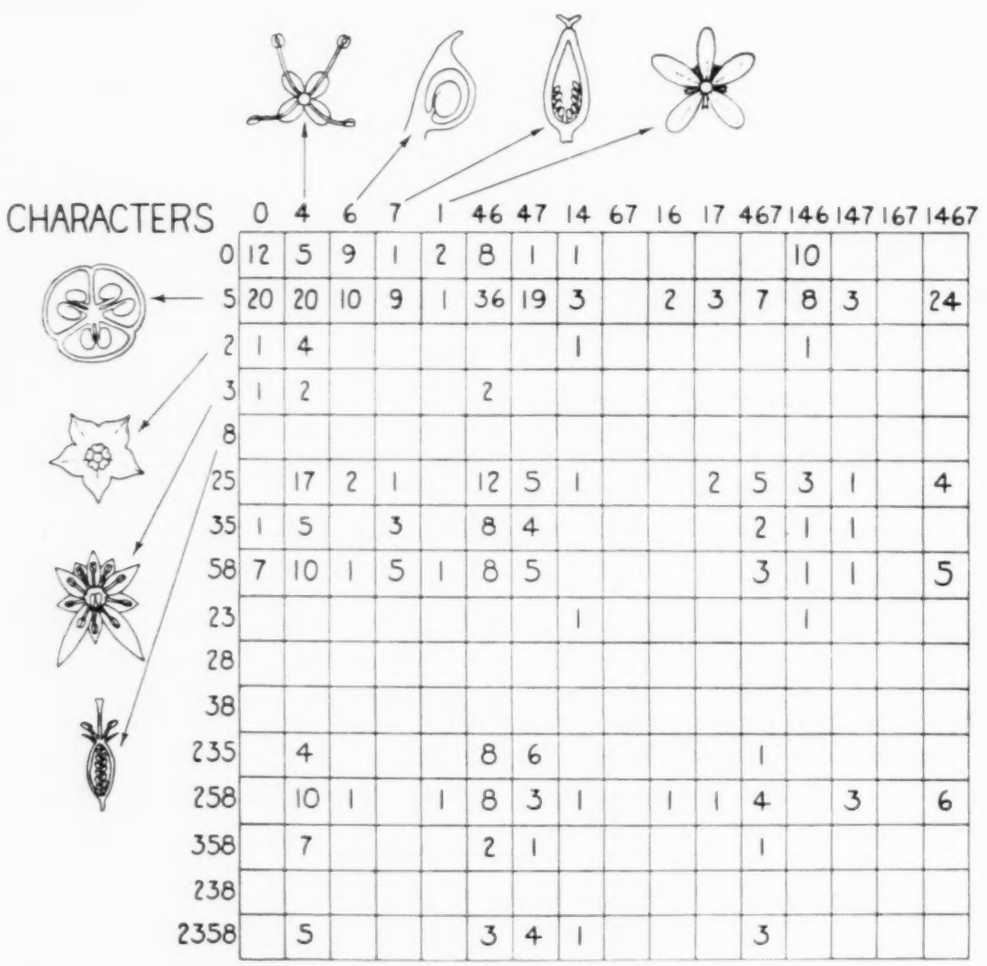

FIG. 1. Chart showing distribution of combinations of eight diagnostic characters among the families of angiosperms. Further explanation in the text.

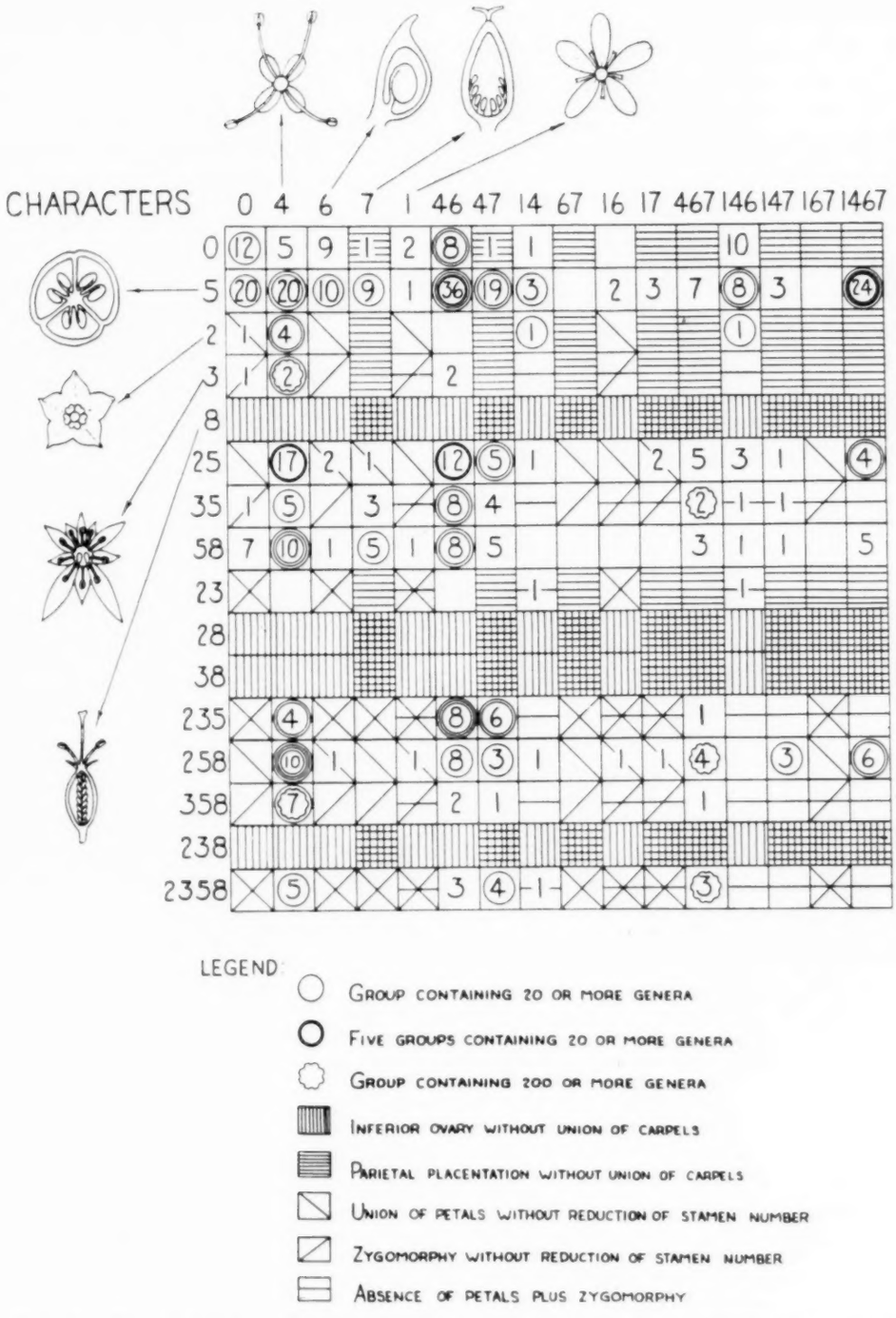

FIG. 2. Chart showing distribution of combinations of eight diagnostic characters among the families of angiosperms. Further explanation in the text.

types of lines placed in most of the unoccupied squares indicate various structurally impossible or apparently unadaptive combinations; these will be explained below.

The chart may therefore be read about as follows. The square in the upper left hand corner, headed by the columns 0 and 0, contains the number 12 surrounded by a single thin circle. This indicates that, as can be verified from table 2, the primitive condition in all eight characters

is possessed by twelve groups, one of them containing more than twenty genera. Near the upper right hand corner, in the square formed by the vertical column headed 1467 and the horizontal one headed 5, appears the number 24 surrounded by one thick circle and two thin ones. This indicates that the condition monochlamydy, polysepaly, actinomorphy, reduction in stamen number, syncarpy, reduction in ovule number, basal placentation, and hypogyny or perigyny, is possessed by twenty-four groups, seven of which contain twenty or more genera. The square in the lower right hand corner contains no number, but only a single horizontal line. This indicates that the advanced condition in respect to all eight characters is not realized by any groups, and that this condition is probably unadaptive or poorly adaptive because it combines the absence of petals with the presence of a zygomorphic flower.

Obviously, this chart could be made up in a very large number of different ways, depending upon the arrangement of the numbers at the heads of the columns. Two different arrangements were made, which produced recognizably but not fundamentally different patterns of arrangement of the numbers. The one used is based on the following scheme. The characters 4, 6, 7 and 1, which head the vertical columns represent in the advanced condition various types of phylogenetic reduction; while the characters heading the horizontal columns, namely 5, 2, 3, and 8, are those representing union of parts or change of symmetry. The serial order of the numbers and combinations of numbers is according to the degree of representation of the combinations; so that the most strongly represented combinations of, say, three advanced characters appear above and to the left of the more weakly represented ones. This arrangement has the advantage of placing next to each other in the largest possible number of instances combinations which differ by only one character. Obviously, all groups differing by a single character could be placed next to each other only in a chart containing several dimensions.

Evidence for the Presence of Adaptive Peaks

Figure 1 brings out in a striking manner the fact that certain combinations of characters are far more frequent than others. Of the 256 combinations of the eight characters selected, only 86 are realized, and 37 of these are represented by only one or two groups. Of the 438 groups (families or part families) 200 are contained in only twelve combinations, or less than five per cent of the total number possible. On the other hand, certain combinations are represented by a large number of groups, the highest numbers being 36, 24, and 20.

The question which arises immediately is: are these inequalities in distribution purely the result of chance, or can the combinations represented by many groups be looked upon as adaptive "peaks," and those occupied by few or none as inadaptive "valleys." Evidence for the latter point of view can be obtained from the nature of both the "peaks" and the "valleys," but the latter will be considered first. Many of the squares are unoccupied because they represent one or both of two types of character combinations which are either structurally impossible or nearly so. These are inferior ovaries without union of carpels (indicated by squares containing parallel vertical lines) and parietal placentation without union of carpels (indicated by squares containing parallel horizontal lines). In addition, there are three types of combinations which, although structurally possible, are found so rarely that they are apparently poor adaptations, usually of low survival value. These are union of petals without reduction of stamen number, marked by a diagonal line passing downward to the right (\); zygomorphy (irregular corollas) without reduction of stamen number, marked by a diagonal line passing

downward to the left (/); and absence of petals combined with zygomorphy, marked with a single horizontal line (—). The non-adaptive character of these three types of combinations can be explained on a functional basis. Both union of petals and zygomorphy are usually associated with pollination of the flower by specialized types of insects and other animals. Cross pollination of flowers by these agents is carried out efficiently only if the stamens are in a very definite position with reference to the style. This precise placing of the stamens is likely to be achieved only if they are of a definite number; hence flowers with united petals or irregular corollas are much more likely to be good adaptations if their stamens are few in number and definite in position. Since absence of petals is usually associated with pollination by wind, and zygomorphy with animal pollination, it is not strange that these two tendencies are rarely associated with each other.

The remaining "valleys," shown on the chart as squares which do not contain markings of any kind, can be explained by comparing the combinations which they represent with other combinations which have been realized by a number of groups. These explanations are as follows.

The combination 16, namely absence of petals, separate carpels, reduction in ovule number together with numerous stamens, is similar to 146, except that in the latter the stamens are also reduced in number. This latter combination is realized by ten small families, including the Platanaceae, Juncaginaceae, Sparganiaceae, and Typhaceae. These are all wind pollinated types in which numerous stamens could hardly be considered a selective disadvantage; in fact these groups have acquired, through aggregation of the flowers, a large number of stamens per inflorescence. The small number of stamens per flower is best regarded as an example of developmental correlation in gene action. Some of the genes which reduced the size and number of the members of the perianth, as well as the number of ovules per carpel, probably acted also to reduce the number of stamens per flower. The unrepresented combination 1567 (petals absent, carpels united with one basal or apical ovule per ovary, stamens numerous) has a similar relationship to the combination 14567, represented by twenty-four groups.

Another series of unrepresented character combinations, namely 567, 5678, 1567, 1568, and 15678, can probably be explained on the hypothesis that genetic factors causing reduction in the perianth and gynaecium are likely to affect also the number of stamens. All of the similar combinations possessing few stamens (4567, 45678, 14567, 14568, and 145678) are more or less well represented.

The combination 1458 (petals absent, carpels united, ovules numerous with axial placentation, ovary inferior) is most similar to 458, found in the Onagraceae, Melastomaceae, and Iridaceae. In these families, which have flowers highly adapted to animal pollination, it is likely that loss of petals would be a selective disadvantage.

The "peaks" are of two types, those occupied by a large number of small, medium sized, or moderately large groups, and those occupied by one very large group plus a few smaller ones. When the family composition of these peaks is examined, as shown in table 2, the fact becomes evident that the families composing most of them have certain characteristics in common. For instance, the largest peak, that at 456 (petals present, separate, corolla regular, stamens few, carpels united, ovules few, placentation axial or basal in separate loculi, hypogynous or perigynous), contains mostly woody families, many of which are tropical or subtropical. Although nearly all of them belong to a series of orders usually regarded as interrelated, such as the Geraniales, Sapindales, and Rhamnales, by no means all of the families in these orders are included. Furthermore, it

seems likely that the condition of one ovule per carpel has been acquired independently in members of different families such as the Ochnaceae, Rutaceae, Meliaceae, and Sapindaceae. Thus most of the families occupying this peak appear to have acquired their similar characteristics partly through relationship, and partly through parallel evolution. In addition, the peak is occupied by four families of monocotyledons, belonging to three unrelated orders. It has therefore been "climbed" several different times, and seems to be a highly adaptive combination under some circumstances, and one which is relatively easily acquired.

A neighboring peak, 457, which differs from the one just described only in possessing parietal placentation and numerous ovules, is occupied by groups of an entirely different type. The great majority are herbaceous, a relatively high proportion are temperate in distribution, and most of them contain rather few genera. They belong to a great variety of different unrelated orders. From these facts, one might suggest that this peak is relatively easy to "climb," and is moderately adaptive for herbaceous types, but relatively inadaptive for woody ones. A peak occupied by similar unrelated groups is the one at 245 (corolla present, petals united, actinomorphic, stamens few, syncarpous, ovules numerous, axile placentation, ovary superior).

The final peak of the first type to be mentioned is that at 14567 (apetalous, actinomorphic, stamens few, carpels united, ovule one with basal or apical placentation, ovary superior). The distribution of woody and herbaceous types among the groups occupying this peak is about the same as among the angiosperms as a whole, and many unrelated orders of both dicotyledons and monocotyledons are represented. Furthermore, an unusually large number of families occupying this peak are relatively large (Piperaceae, Polygonaceae, Chenopodiaceae, Amaranthaceae, Moraceae, Araceae, Palmae, Cyperaceae). Most of them are wind pollinated, and many of those which are insect pollinated (Araceae, *Ficus*) seem to have acquired this characteristic secondarily from wind- or water-pollinated ancestors. Nearly all of them have numerous small flowers aggregated into dense inflorescences.

The "peaks" of the second type, those occupied by one very large group plus a few small ones, are five in number. The most primitive, 34, is occupied by the Caesalpiniaceae and Papilionaceae, which are often grouped together under the family Leguminosae. This family is undoubtedly relatively old, and may have exploited this adaptive combination so early in the evolution of the angiosperms that no other family was able to compete with it on its own ground. The adaptiveness of the leguminous flower seems to lie in the fact that it can be relatively easily adapted to pollination by a variety of different insects and birds, while the leguminous pod can become modified for various agencies of seed dispersal.

The peak 3458, occupied by the very large family Orchidaceae, is shared by a few small unrelated part families and one whole family of monocotyledons (*Phylidraceae, Cannaceae, Iridaceae, Amaryllidaceae, Alstroemeriaceae*), and by a few genera of Melastomaceae among the dicotyledons. The orchids were probably the first to "climb" this rather specialized peak, and their great success may have kept other groups from exploiting this combination successfully.

The peak 34567, occupied by the Gramineae, is a very unusual one for a wind pollinated group. Its only companion on this peak is a part of the Fumariaceae, which are strongly modified for insect pollination. Most of the neighboring combinations are poorly represented. The most strongly represented one, 3456, is occupied by families like the Polygalaceae, Balsaminaceae, and Sapindaceae, which also have flowers highly modified for animal pollination. The Gramineae are placed in their combination because of the lodicules, which are

regarded as modified petals, and the palea, which may represent the union of two sepals. These structures, plus those of the inflorescence, give the grass flower a distinct bilateral symmetry, in contrast to the flowers of most other wind pollinated plants. But whereas bilateral symmetry or zygomorphy is in most angiosperms an adaptation for animal pollination, in the grasses it appears to be an adaptation for the quick opening and closing of the flower in response to slight changes in moisture and temperature. The lodicules are particularly efficient in this respect. This ability may be largely responsible for the much greater success which the grasses have achieved under dry conditions, as compared to other wind pollinated, narrow leaved monocotyledons, such as the Cyperaceae, Juncaceae, and Restioneaceae.

The final two peaks to be discussed are 245678 and 2345678, both occupied by the Compositae plus a few small families usually associated with them (Calyceraceae, Valerianaceae, Dipsacaceae). These peaks, which represent the highest degree of specialization of the angiosperm flower and fruit, were probably "climbed" by the ancestral Compositae at a relatively early date in the evolution of the angiosperms; evidence of the age of this family is presented elsewhere (Stebbins, 1941). In this case, also, direct competition with the highly successful Compositae probably prevented members of other groups from exploiting extensively this highly adaptive combination of characters.

Association Between Individual Characteristics

Another type of evidence which favors the hypothesis that combinations of characters which occur frequently are the ones which are highly adaptive is derived from a study of associations between pairs of individual characteristics. Such associations were calculated by the chi square method, essentially as described by Sporne (1949). The results of these calculations are presented in table 3.

The first generalization evident from this table is that the woody habit shows negative association with the advanced condition in respect to six out of the eight characters studied. In other words, herbaceous angiosperms tend to have more specialized flowers than woody ones, a fact generally recognized by systematists and morphologists. The two exceptional characters deserve attention. The woody habit shows a highly significant association with the reduction of the ovules to one per carpel or one per flower; and no significant association with apetaly. Two explanations might be given for these exceptions. One would be the possibility that the two characters concerned have been wrongly interpreted, and that one ovule per carpel as well as apetaly are primitive rather than derived conditions. In respect to the former character, the anatomical evidence is entirely against such an interpretation, as has been pointed out by Eames (1931) and numerous other workers. Furthermore, the larger families which have consistently a much reduced number of ovules (Polygonaceae, Chenopodiaceae, Fagaceae, Umbelliferae, Boraginaceae, Labiatae, Compositae, Cyperaceae, Gramineae) are also highly specialized in other characteristics, while within such families as the Rosaceae, Leguminosae, and Rubiaceae, the genera with reduced numbers of ovules are in general more specialized than those with numerous ones. In respect to apetaly or monochlamydy, the situation is not so clear. This condition is also considered as derived by most students of plant anatomy, and the presence of occasional genera or species with apetalous flowers in otherwise polypetalous families (*Chrysosplenium,* Saxifragaceae; *Sanguisorba, Cercocarpus,* and *Cowania,* Rosaceae; species of *Stellaria* and *Sagina,* Caryophyllaceae) is further indication that this condition is in many instances, if not always, a derived one. Furthermore, apetaly shows positive association with

TABLE 3. *Association between the principal characters studied.* The symbols in each square represent the degree of association between the characters designated at the beginnings of the columns leading to that square. The symbol 0 indicates no significant association ($p > .05$); the symbols + and − indicate respectively significant positive and negative associations ($p = 0.01$–0.05); the symbols ++ and −− indicate respectively highly significant positive and negative associations ($p < 0.01$).

	Woody habit	Epigyny	Parietal basal placent.	Red. no. ovules	Syn-carpy	Red. no. stamens	Zygo-morphy	Sym-petaly
Apetaly	0	0	++	++	0	+	−−	0
Sympetaly	−−	++	0	0	++	++	++	
Zygomorphy	−−	0	0	−	0	++		
Reduced no. of stamens	−−	0	+	++	++			
Syncarpy	−	++	++	++				
Reduced no. of ovules	++	0	+					
Parietal or basal placentation	−−	0						
Epigyny	−−							

three of the other seven character conditions assumed to be advanced, and negative association with only one of them.

The other most likely possibility is that the association between most primitive floral characteristics and the woody habit is due not simply to the fact that all of these characteristics are primitive, as Sporne (1949) has assumed, but has a selective basis. On the basis of this assumption, the deduction could be made that reduction of ovule number is the only advanced characteristic being considered in this paper which has a high selective value when combined with the woody habit more often than when combined with the herbaceous habit. This assumption and deduction will be considered in turn.

Woody plants might be expected, on the average, to have less specialized flowers than herbaceous ones because in woody plants the relatively great length of life of the individual reduces the selective value of an efficient reproductive system in comparison with an efficient vegetative system. The writer has previously pointed out (Stebbins, 1950, pp. 137–143) the fact that in both the Compositae and Gramineae, and presumably other families, short-lived annual herbs tend to have more efficient reproductive systems

as compared to their longer lived relatives. A similar interpretation can be given to the situation in the "woody" Gramineae, the bamboos. These grasses have more generalized, primitive flowers than any others, and were believed by Bews (1929) to represent the most primitive types of the family. However, their vegetative structure is far from primitive, in relation to that of other grasses, and there are no members of other monocotyledonous families which resemble them in any way. The Bambuseae, therefore, are looked upon by the present writer not as the original prototypes of the grasses or as their unaltered descendants, but as grasses which have become highly specialized in vegetative structures while retaining a relatively primitive type of flower. Since flowering and seed setting is rare and sporadic in the great majority of species of Bambuseae, the opportunity for natural selection to act in the direction of increasing the efficiency of reproductive structures would be particularly slight in this group. We can suggest, therefore, that many groups of woody plants have been able to persist because of their efficient vegetative systems, and in spite of relatively inefficient, unspecialized systems of reproduction.

If this were the case, then we should expect that certain individual specialized characteristics of the reproductive system, which had a particularly high selective value in connection with the woody habit, would be present in woody groups more often than in herbaceous ones. Reduction in number of ovules per flower might be such a character.

There are two reasons why reduction in ovule number would have a selective advantage in woody plants. First, woody species have, on the average, larger seeds than herbaceous ones. This may be associated in many instances with the slower development of the seedling, and the value of a large amount of stored food, thus permitting the seedling to develop an extensive root system before a large photosynthetic surface is available, but other reasons may also exist for these larger seeds of woody plants. As pointed out elsewhere (Stebbins, 1950, p. 132) genes acting to increase seed size may also act to reduce the number of ovules per carpel. A second reason for the reduction of ovule number in woody species is the fact that many of the deciduous types, particularly in temperate regions and in the drier parts of the tropics, develop flowers relatively rapidly, before the leaves appear. Under such conditions, reduction in flower size, which might carry along with it reduction in number of ovules, would aid in the rapid development of the flower.

The reduction and disappearance of the corolla probably has as great a selective value in woody plants as in herbaceous ones for two reasons. The first, already mentioned, is the selective advantage in many trees and shrubs of general reduction in flower size, accompanied by increasing rapidity in floral development. The second is the high frequency of wind pollinated flowers, particularly among the trees and shrubs of temperate regions. The absence of petals in most wind pollinated flowers is a well known fact.

The only generalization possible about the associations between different pairs of the reproductive characters concerned is that no single character is significantly associated with all of the other seven. Furthermore, three of the eight, apetaly, zygomorphy, and reduction in ovule number, are positively associated with some, and negatively associated with others of the seven remaining characters.

This situation is particularly noteworthy in respect to zygomorphy, or irregular flowers, a character which every systematist recognizes as advanced and specialized. It shows highly significant positive association with union of petals and reduction in stamen number; no significant association with united vs. separate carpels, parietal vs. axial placentation, or epigyny vs. hypogyny or perigyny; a significant negative association with reduction in ovule number, and a highly

significant negative association with apetaly. All of these significant associations can be explained as adaptive character combinations. Most zygomorphic flowers are highly modified for animal pollination. In such flowers, a united perianth and a reduced number of stamens both make possible a larger number of adaptive devices for ensuring the visits of the pollinating organism and successful cross pollination. The negative association with reduced ovule number; i.e., a positive association with many seeds per flower, is probably also connected with adaptation to animal pollination. Many plant groups highly specialized for cross pollination by insects and other animals, like the Orchidaceae, Asclepiadaceae, and Aristolochiaceae, are in a way overspecialized. Their devices to secure cross pollination, with its consequent maintenance of genetic heterozygosity, are so highly specialized that they do not always function, and many flowers fail to set any seed. In such plants, the selective advantage of a flower in which a single act of pollination causes many ovules to be fertilized is obvious. Nevertheless, this association is not highly significant, as is attested by the presence of several large families (Labiatae, Compositae) in which zygomorphy is combined with reduction in ovule number. In these families, aggregation of the flowers into dense inflorescences may provide sufficient assurance of abundant seed formation, in spite of the small number of ovules fertilized with each act of pollination.

The highly significant negative association between zygomorphy and apetaly may be explained by the fact that apetaly is usually an adaptation for wind pollination, while zygomorphy is usually an adaptation for animal pollination. The two conditions rarely make a harmonious combination.

The data presented above show clearly that the basic assumption recently made by Sporne (1949) in his "new approach to the problem of the primitive flower" does not hold. He suggested that "correlations" (which in this paper are termed associations, a more appropriate term in the writer's opinion) "between floral and vegetative characters could be used in assessing the relative advancement of families of Dicotyledons. . . ." This is considered possible because "any two primitive characters can be shown to occur together more frequently than they would be if distributed at random throughout the flora." The present writer has shown that the primitive characters of woody habit and numerous ovules per carpel, as well as those of presence of petals and regular corollas, occur together far *less* frequently than if distributed at random. This is part of a process of adaptive radiation, similar to evolutionary tendencies in other organisms. We could say that in many instances evolution of the herbaceous habit tends to reduce the selective value of evolution toward reduction in ovule number. Also, evolution toward wind pollination and apetaly reduces the selective value of zygomorphy, which represents an entirely different type of adaptive radiation.

The problem of the primitive flower cannot be settled by statistics alone. It will require pooling the evidence from morphology, anatomy, development, geographic distribution, and paleobotany, as well as considerations of the selective value of character combinations, and individual phylogenies in particular families. At present the writer suggests only that his evidence tends to agree with that of those systematists and morphologists, such as Bentham and Hooker, Bessey, and Hutchinson, who consider that the primitive condition is the insect pollinated "perfect" flower with separate, spirally arranged parts, as found in many of the Ranales. All of the other types appear to have been derived from such primitive ancestors by a series of adaptive radiations, including divergences, convergences, and numerous examples of parallel evolution.

General Adaptive Trends in the Angiosperm Flower

The present study suggests the existence of four principal adaptive trends in the angiosperm flower. These are as follows: First, increase in rate of development of flowers and fruits, which is largely responsible for reduction and fusion of floral parts. Second, special adaptations for insect or bird pollination the most widespread of which are the union of sepals and petals, the development of irregular corollas, and of inferior ovaries. Third, special adaptations for wind pollination, the principal ones of which are reduction of perianth parts and separation of the sexes. Fourth, adaptations for various types of seed dispersal and the establishment of seedlings under various conditions. These adaptations affect primarily the size of the seeds, and various appendages of these seeds and fruits, and secondarily the number of seeds per flower, as well as their placentation. These four trends will be discussed in turn.

The significance of increase in rate of development of flowers and fruits has been discussed previously by the writer (Stebbins, 1950, pp. 507–508). Its adaptive value is particularly great in arid areas, and in cool temperate or boreal regions with extreme seasonal differences. The fewer and the more reduced in size are the parts of a flower, the more rapidly can the flower develop. Furthermore, the union of parts reduces the number of growth centers that are present, and so contributes also to speeding up rates of development. Many plants compensate for the loss of productivity in seeds or pollen which this reduction might bring about by the aggregation of the flowers into complex inflorescences.

Adaptation to insect or bird pollination is generally recognized to be responsible for union of petals, and for the various types of zygomorphic or irregular corollas. Furthermore, extreme adaptation in this direction, which tends to keep the visits of one type of pollinator confined to a single species, and so to reduce the formation of unproductive interspecific hybrids, is responsible for various unusual modifications of the perianth and stamens, such as are found in the Orchidaceae and Asclepiadaceae (Stebbins, 1950, pp. 210–213). In a recent publication Grant (1950) has suggested that inferior ovaries, as well as the union of stamens and other modifications of the flower, have arisen as protective devices against biting insects and birds, which are the regular pollinators of many flowers possessing such devices, and which might otherwise seriously damage the developing ovules.

Adaptation to wind or water pollination is probably responsible for most examples of apetaly or haplochlamydy among the modern angiosperms, and also for the evolution of imperfect, monoecious or dioecious flowers. This is quite clear in the case of many such examples known to the writer in which the nearest relatives of the apetalous, monoecious, or dioecious groups are known. The Cyperaceae, Gramineae (*Buchloe, Zizania, Zea*), various genera of Anacardiaceae, the genus *Thalictrum* of the Ranunculaceae and the tribe Ambrosieae of the Compositae can be cited as examples. In view of this fact, and also of the now generally accepted fact that the various families originally placed together as the Amentiferae are actually of very different affinities, the writer is inclined to accept the abundant evidence from floral anatomy (Abbe, 1935; Berridge, 1914; Boothroyd, 1930; Fisher, 1928; Manning, 1940; Mosely, 1948) which points to the advanced position of all of these families. Sporne (1949) has suggested that the primitive angiosperm flower was unisexual, and believes that the Fagaceae and Salicaceae are the most primitive modern unisexual descendants of these original angiosperms. According to the criteria of the present writer, the Salicaceae occupy an intermediate position, in the groups 157 and 1457; while the

Fagaceae, in the group 145678, are highly specialized. In the case of the latter family, the evidence of Berridge (1914) on the relatively primitive genus *Castanopsis,* and personal observations on the equally primitive genus *Lithocarpus* indicate that both of these genera form a few perfect flowers more or less regularly, and strongly suggest that the unisexuality in the flowers of the Fagaceae is a derived condition. Sporne considers the flowers of the Salicaceae to be "fundamentally unisexual," but the anatomical evidence of Fisher (1928) is strong indication that the flowers in this family are likewise reduced from types which had a perianth and were bisexual.

Considerable diversification of the angiosperm flower has apparently been produced by the reversion to entomophily of groups previously specialized for wind pollination. The complex, showy inflorescence of species of *Euphorbia* are perhaps the most striking examples of this trend, but other genera of the Euphorbiaceae (*Ricinus, Hevea*), as well as the Nyctaginaceae, Araceae, and possibly Aristolochiaceae are probable additional examples.

In regard to seed dispersal, the mechanisms of various types of appendages, as well as fleshy fruits, are so well known that they need not be discussed here. In respect to these structures, also, some types of reversal exist. For instance, the pappus was probably developed early in the evolution of the Compositae or their ancestors as a means of seed dispersal, but it has become lost in many modern, specialized genera of the family. Significantly, the genera in which this has happened are mostly those with rather small seeds, such as the tribe Anthemidae, or with the involucral phyllaries specialized for seed dispersal, as in the tribe Ambrosieae and the genus *Madia.* In these groups, wide dispersal of seed can be carried out without the aid of a pappus.

The importance of seed size in relation to habitat and the establishment of seedlings was fully discussed by Salisbury (1942) in relation to the British flora. Further comments were added by the writer (Stebbins, 1950, pp. 134–136), who pointed out that this factor of seed size affects the relative frequency of members of different plant families in meadow, shrub, and woodland habitats. The family characteristics most strongly affected by seed size are, as pointed out above, placentation and the number of seeds per carpel or per flower. If the seeds are very large, such as those of *Juglans* and *Aesculus,* there simply cannot be very many in an ovary. An ovary bearing seeds the size of these genera, say one cubic inch per seed, and containing as many seeds as the capsule of *Nicotiana* (300,000), would have to be five feet in diameter and seven feet high!

These considerations suggest a possible selective basis for the evolution of exalbuminous seeds, in which the stored food material is contained within the cotyledons. The groups which have this characteristic have for the most part large seeds, and relatively few per flower. Under such conditions, the efficient germination of the seeds, and the establishment of a relatively large percentage of seedlings, might have a much greater selective value than it would in species which produce a very large number of seeds. Food stored in the cotyledons should be more easily available to the germinating seed than the ordinary endosperm which surrounds the embryo.

When all of these facts are considered, the evidence for the selective basis of the evolution of the flower and fruit seems sufficiently strong to deserve more serious consideration as well as further observation and experimentation to verify such hypotheses as the ones presented above. The writer has suggested elsewhere (1950, p. 506) that the differentiation of the families of flowering plants is an example of adaptative radiation which differs quantitatively but not qualitatively from the well known examples of this phenomenon in animals. The present evidence tends to support and amplify this hypothesis.

Summary

Comparison of the characteristics of the flower and fruit in several families of angiosperms has led the writer to the working hypothesis that the combinations of characteristics found in the larger, more successful families of flowering plants evolved through the guidance of natural selection because they represented particularly successful methods of solving problems of fertilization, seed dispersal, or both. Evidence to support this hypothesis was obtained by classifying all of the families of angiosperms as primitive or advanced in respect to the following eight characters: presence vs. absence of petals; polypetaly vs. sympetaly; actinomorphy vs. zygomorphy; numerous vs. few stamens; apocarpy vs. syncarpy; numerous vs. few ovules; axile vs. parietal apical, or basal placentation; and hypogyny or perigyny vs. epigyny. Of the 256 possible combinations of these characters, only 86 are represented by one or more family or part family. Nearly half (200) of the 438 families and part families classified fell into one of twelve combinations, indicating a still stronger deviation from random representation of the different combinations. Nearly all of the character combinations not found in any group are either structurally impossible or can be seen clearly to be inadaptive. Most of the combinations which are strongly represented occur in groups which resemble each other to some degree in vegetative characteristics, but which nevertheless are not in all cases closely related. The combinations found in the largest families of angiosperms (Compositae, Leguminosae, Gramineae, Orchidaceae) are found in few or no other families; evidence that the successful exploitation of these combinations by other groups has been retarded by competition with the large families which first acquired them.

Six of the eight advanced characters are negatively associated with the woody habit, one is positively associated and one, apetaly, shows no significant association. The positive association between the woody habit and reduction in number of ovules per carpel is probably due to the greater selective value of large seed size in many woody plants, and to a secondary effect of genes causing increase in seed size. Most of the eight advanced characters are positively associated with each other, but there are some instances of non-association and two of negative association. These can be explained on a selective basis. Four general adaptive trends in floral evolution are as follows: 1, toward reduction and union of parts, with consequent increased rapidity of development; 2, toward greater specialization for insect and bird pollination; 3, toward specialization for wind and water pollination; 4, special adaptations for seed dispersal and establishment of seedlings, the latter affecting size and number of seeds.

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A MATHEMATICAL MODEL APPLIED TO A STUDY OF THE EVOLUTION OF SPECIES

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INTRODUCTION

This paper presents a mathematical model that is believed to be applicable to the solution of certain fundamental problems of evolution. Its use is illustrated by the study of a particular problem. Attention is focused upon the nature of morphological change at a low taxonomic level including analyses of the mechanism and modes of these changes. The data that modern experimental and analytical methodology can provide are as yet insufficient for comprehensive answers to all phases of problems of this type and severe restrictions are imposed when, as in the illustration, investigations are limited to part of a single anatomical system of extinct organisms. Nevertheless, much of interest and significance may be gained by carefully planned exploitation of the data that are available.

Certain taxonomic problems have proved especially amenable to solution by statistical procedures but, mostly, results are either supplementary or complementary to those achieved by other methods of study. There are, however, many problems of evolution that cannot be treated adequately by classical approaches or by application of the statistical procedures now commonly used by students whose data are primarily morphological. Among these are problems concerned with the intricate, small morphological modifications that occur in the evolution of subspecies and species. By use of the method outlined here we hope to detect and describe such changes, thus adding to an understanding of the nature of differences separating small taxonomic units, and also, more importantly, to draw inferences concerning factors that have operated to produce these changes.

The characters treated in numerical studies, such as the one considered here, are necessarily dimensions. A serious difficulty in many analyses of the nature of change stems from the tendency to treat modifications of each dimension, as if they were independent of other modifications, whereas intimate interdependence actually exists. Much information, on the other hand, is lost if various changing dimensions are treated together in a way that masks the importance of individual contributions to the whole. Most profitable would be a search for some unifying principle under which each changing part can be studied in relation to its effects on other changing parts, whether these be closely related or partially or completely independent. Such a principle, involving the concept of closely related groups of measurements, has been developed and demonstrated in work, as yet unpublished, by the junior author. We may hope by its use as demonstrated here to approach a little more closely to an organismic basis for analysis of change in evolution, and to provide more definite bases for determining how and why particular changes came about, than has been possible in the past.

The problem considered here concerns three closely related species of early Permian reptiles of the Family Captorhinidae, whose essentially contemporaneous existence implies a not remote common ancestor. The acceptance of this implication is the basis for inquiry concerning changes that have probably taken place in the evolution of descendant species, although the ancestral stock is unknown.

Mr. William Kruskal, a member of the Committee on Statistics of the University of Chicago, has given much time

and invaluable assistance in the development and statement of the mathematical portions of the paper. Mr. Bryan Patterson and Dr. J. Marvin Weller, of the Chicago Natural History Museum and the University of Chicago respectively, have critically read the paper and offered suggestions that have been incorporated. We express our deep appreciation for their aid.

The samples studied have been assembled from the collections of The American Museum of Natural History, The Museum of Comparative Zoology of Harvard University, The University of Oklahoma and The Chicago Natural History Museum. We are grateful to these institutions for permission to study their collections.

Materials and Measurement

Samples of populations of three captorinomorph reptiles, *Captorhinus aguti*, *Labidosaurus hamatus* and *Labidosaurus* sp., constitute the material studied. These are referred to as Species 1, Species 2 and Species 3 respectively in later discussions. Generic separation of *Captorhinus* and *Labidosaurus* is based primarily on the maxillary and dentary dentitions. *Captorhinus* has multiple rows of teeth whereas *Labidosaurus* has but a single row. On this basis Species 3, an unnamed species, has been assigned to the genus *Labidosaurus*. In the present work, however, generic distinction is not of primary concern and categorization at this level on the basis of the nature of dentition tends to obscure the objectives. Dental modifications represent but one of many changes that presumably took place in differentiation of the three species from their common ancestor and are not independent of these other changes. For the purposes of this study, the three species are considered without regard to generic position.

The sample of *Captorhinus aguti* consists of 43 whole or partial skulls, largely from the Arroyo formation of Texas and beds of equivalent age in Oklahoma. A few specimens from the Admiral, Belle Plains and Clyde formations of Texas are included. Study has shown that most known specimens of *Captorhinus* may be properly referred to this species. The sample of *Labidosaurus hamatus* consists of 14 skulls, all from the Arroyo formation of Texas. The sample of *Labidosaurus* sp. includes 7 skulls or partial skulls from the Wellington formation of Oklahoma, an Arroyo equivalent, and was supplied by Dr. J. Willis Stovall of the University of Oklahoma.

All measurements are in millimeters to either the closest whole or 1/10th millimeter as is appropriate. They were made upon the dorsal dermal surfaces of the skulls. Eight measurements were taken on as many specimens as possible, but breakage and excessive distortion have consistently reduced the number of measurements below the number of specimens. The size of the samples is small and accordingly appropriate safeguards for small sample statistics have been used.

The measurements used are as follows:

Skull Length (Sk_1): The distance along the midline of the skull from the posterior margin of the dorsal platform to the tip of the snout on a plane parallel to the surface of the dorsal platform.

Orbito-Snout Length ($O–S_1$): The distance along the midline of the skull from a vertical plane tangent to the anterior margins of the orbits to the tip of the snout on a plane parallel to the dorsal platform.

Nasal Length (Na_1): The distance along the midline of the skull from the suture between the frontal and nasal to the suture between the premaxillary and the nasal.

Frontal Length (Fr_1): The distance along the midline of the skull from the suture between the nasal and the frontal to the suture between the parietal and the frontal.

Parietal Length (Pa_1): The distance along the midline of the skull from the

suture between the frontal and the parietal to the posterior end of the dorsal platform.

Orbital Length (O_1): The maximum distance between the anterior and posterior margins of the orbit on a plane parallel to the dorsal platform of the skull.

Interorbital Width (Io_w): The minimum distance between the dorsal margins of the orbits on a line normal to the midline of the skull.

Maxillary Tooth Row Length (Tr_1): The distance along a straight line between the most posterior and most anterior marginal maxillary tooth.

The abbreviations given in the above list are used throughout the remainder of the paper to specify the particular measurements.

The Model: Concept of Morphological Sets

The General Case

A model has been constructed for the general case so that the complexities that result from handling interrelationships of measures can be treated in a logical and economical manner. The procedures and interpretations in the specific problem attacked here were chosen in accordance with the model. It is hoped that this model will prove useful in attacking other problems of a similar nature. The fundamental reasoning is as follows:

1. Each measurement of an individual is related to every other measurement and the relationship can be expressed numerically as a correlation coefficient if a group of individuals (i.e. a species) is considered. (The degree of association may be expressed numerically as greater than or equal to 0.)

2. The totality of measurements can be arranged in highly intercorrelated groups.

3. These groups have biological significance and are formed in part under the influence of functional and/or developmental patterns.

The morphological characters of a group of organisms, presumably a species, may be conveniently and usefully treated in terms of measurements as follows:

A. Mathematical considerations.

1. Let $X_1, X_2, \ldots,$ represent the various measures taken on a species. Measure is defined as a quantitative characteristic of a population, or species.

2. Each of these measures has a numerical correlation $\geqslant 0$ with each of the other measures.

If we think of the measures as forming a large group or "set," it is possible in an ideal case to form subdivisions of the set by using the criterion that the intercorrelation of the members of the set be equal to or greater than an arbitrarily chosen correlation value.[1] The choice of the correlation value is made so as to break the set of measures up into groups, and is based on the assumption that groups of intercorrelated measures have biological significance. The result is the formation of subsets of measures, all intercorrelated at the level of ρ that most clearly delineates discrete groups. These are called ρ-groups. Certain measures may be common to several of the groups and to this extent the ρ-groups overlap each other.

B. Biological considerations.

1. Consider, as above, the various measures which have been taken on a species.

2. Many of these measures may be grouped together on the basis of function, such as mastication, or in terms of some developmental pattern. The groups formed in this way are called F-groups.

[1] In a particular case, this optimum condition may not be realized. For example, there may be incomplete coverage of the animal in terms of measurements, or there may be a masking interaction of biological factors. As a result, measures that are correlated with most members of a ρ group at the proper level are included.

A ρF-group is defined as the combination of a ρ-group with an F-group and thus is dependent on mathematical relationships and on biological considerations. These ρF-groups form the basis for comparison of species, in a horizontal (geographic or environmental) sense and also in a vertical (time) sense, with regard to evolutionary change.

A more detailed and precise definition of ρ and F groups, and of the combination of these into ρF-groups, will be found in the appendix (p. 337).

TABLE 1. *Summary of r values and partial correlation coefficients.* Symbols: *, indicates not significantly different from O correlation; ′, indicates less than $\rho = .95$.

Species 1

		Pa_1	O_1	Sk_1	Io_w	Na_1	Fr_1	Tr_1
O–S_1	n =	24	31	33	32	22	23	15
	r_{xy} =	.873′	.628′	.896′	.744′	.899	.881	.967
	$r_{xy}.Sk_1$ =	*.128	−.329		*−.172	.366′	*.244	.872
	$r_{xy}.Pa_1$ =	———	*.167		*.082	.574′	.509′	.857′
	$r_{xy}.Io_w$ =	.687′	*.295		———	.754′	.709′	.936
	$r_{xy}.O_1$ =	.786′	———		.571′	.827′	.883	*1.09
Pa_1	n =	25	26	27	20	22	15	
	r_{xy} =	.778′	.956	.826′	.871′	.868′	.923	
	$r_{xy}.Sk_1$ =	*.081		*−.051	*−.274	*−.344	.695′	
	$r_{xy}.Pa_1$ =	———		———	———	———	———	
	$r_{xy}.Io_w$ =	.575′		———	.567′	.588′	.757′	
	$r_{xy}.O_1$ =	.573′		.679′	.699′	.616′	.793′	
O_1	n =	33	34	20	22	15		
	r_{xy} =	.799′	.641′	.738′	.877′	.869′		
	$r_{xy}.Sk_1$ =		*−.191	*−.065	.617′	.595′		
	$r_{xy}.Pa_1$ =		*.006	*.196	.645′	.623′		
	$r_{xy}.Io_w$ =		———	.478′	.801	.786′		
	$r_{xy}.O_1$ =		———	———	———	———		
Sk_1	n =	32	21	24	16			
	r_{xy} =	.872′	.940	.944	.855′			
Io_w	n =	21	22	14				
	r_{xy} =	.851′	.823′	.827′				
	$r_{xy}.Sk_1$ =	*.190	*.004	*.321				
	$r_{xy}.Pa_1$ =	.476′	*.379	*.298				
	$r_{xy}.Io_w$ =	———	———	———				
	$r_{xy}.O_1$ =	.737′	.708′	.711′				
	n =	21	13					
	r_{xy} =	.877′	.927					
	$r_{xy}.Sk_1$ =	*−.089	.687′					
	$r_{xy}.Pa_1$ =	.494′	.652′					
	$r_{xy}.Io_w$ =	.590′	.756′					
	$r_{xy}.O_1$ =	.708′	.855′					
	n =	15						
	r_{xy} =	.906						
	$r_{xy}.Sk_1$ =	.577′						
	$r_{xy}.Pa_1$ =	.547′						
	$r_{xy}.Io_w$ =	.706′						
	$r_{xy}.O_1$ =	.605′						

TABLE 1.—*Continued.*

Species 2

		Pa_1	O_1	Sk_1	Io_w	Na_1	Fr_1	Tr_1
O–S_1	n =	10	10	12	12	10	11	6
	r_{xy} =	.842′	.900	.874	.879	.832′	.882	.784′
	$r_{xy}.Sk_1$ =	*.200	.534′		.569′	*.113	*.459	.909
	$r_{xy}.Pa_1$ =	———	.658′		.566′	*.269	.560′	−.710′
	$r_{xy}.Io_w$ =	*.361	.783′		———	.543′	.562′	*.171
	$r_{xy}.O_1$ =	*.372	———		−.735′	*.153	.439′	*.487
Pa_1	n =		8	10	10	10	10	6
	r_{xy} =		.839	.920	.857	.920	.872	.967
	$r_{xy}.Sk_1$ =		*.083		*.429	*.301	*.270	.894
	$r_{xy}.Pa_1$ =		———		———	———	———	———
	$r_{xy}.Io_w$ =		.597′		———	.811	.550′	.883
	$r_{xy}.O_1$ =		———		.651′	.700′	.520′	.975
O_1	n =			10	10	8	9	6
	r_{xy} =			.896	.736′	.891	.879	.703′
	$r_{xy}.Sk_1$ =				*−.002	*.213	*.386	
	$r_{xy}.Pa_1$ =				*.115	.558′	.558′	−.776′
	$r_{xy}.Io_w$ =				———	.756′	.711′	*.229
	$r_{xy}.O_1$ =				———	———	———	———
Sk_1	n =				12	10	11	6
	r_{xy} =				.830	.968	.897	.985
Io_w	n =					10	11	6
	r_{xy} =					.752′	.837′	.841
	$r_{xy}.Sk_1$ =					*−.360	*.376	*.185
	$r_{xy}.Pa_1$ =					*−.181	*.354	*−.094
	$r_{xy}.Io_w$ =					———	———	———
	$r_{xy}.O_1$ =					*.309	.617′	.667′
Na_1	n =						10	6
	r_{xy} =						.808′	.950
	$r_{xy}.Sk_1$ =						−.538′	*−.059
	$r_{xy}.Pa_1$ =						*.003	*.608
	$r_{xy}.Io_w$ =						*.496	.892
	$r_{xy}.O_1$ =						*.116	1.002
Fr_1	n =							6
	r_{xy} =							.949
	$r_{xy}.Sk_1$ =							.851
	$r_{xy}.Pa_1$ =							.845
	$r_{xy}.Io_w$ =							.827
	$r_{xy}.O_1$ =							.976

The Specific Problem

The specific problem considered here can be handled in terms of this model. As in any real problem, especially one concerned with paleontological materials, the number of measurements available is much smaller than the totality of possible measurements. Nevertheless some hints of the real picture can be gained.

Eight measures were derived from each of the three species. Each species was analyzed in terms of these measures for the purpose of forming groups of the ρF type defined previously. Results of calculations are shown in table 1. The ρ-groups were formed so that all pairs, triplets, etc. were noted. These are shown graphically in figure 1. Biologi-

TABLE 1.—*Continued.*

Species 3

		Pa_1	O_1	Sk_1	Io_w	Na_1	Fr_1	Tr_1
$O–S_1$	n =	4	4	4	6	6	6	4
	r_{xy} =	*.771	.957	.959	.810	.911	.826	.983
Pa_1	n =		5	5	5	5	5	4
	r_{xy} =		.963	.962	*.700	.897	.973	*.753
O_1	n =			5	4	4	4	4
	r_{xy} =			.994	*.742	.947	.936	.921
Sk_1	n =				5	4	5	4
	r_{xy} =				*.702	.987	.934	.956
Io_w	n =					6	5	4
	r_{xy} =					*.750	.827	*.209
Na_1	n =						4	4
	r_{xy} =						.866	.957
Fr_1	n =							4
	r_{xy} =							.773

cal considerations suggest that four of these measures form a functional group related to mastication and these are circled. This is the only F-group that seems reasonable. Since only one F-group can be distinguished, only one ρF-group can be discussed.

Inspection of figure 1 shows that:

1. The ρ-groups differ in Species 1 as compared to Species 2 and Species 3. That is, there are ρ-groups in Species 2 and Species 3 that contain measures not found in any group in Species 1.

2. The entire complex of ρ-groups differs in each of the species, the pattern of interrelationships being different.

3. The situation, except perhaps in Species 1, is too complex to allow discussion of $A_{F_{mast.} \cup A \rho \cdot s}$ in terms of evolutionary change. This group, $\rho F_{mast.}$, will be referred to as the masticatory complex throughout the rest of the paper.

4. In Species 1, Pa_1 and in Species 2 and Species 3, O_1 and Io_w fall outside of F but are in ρ. The association of these measures with those in F may result from

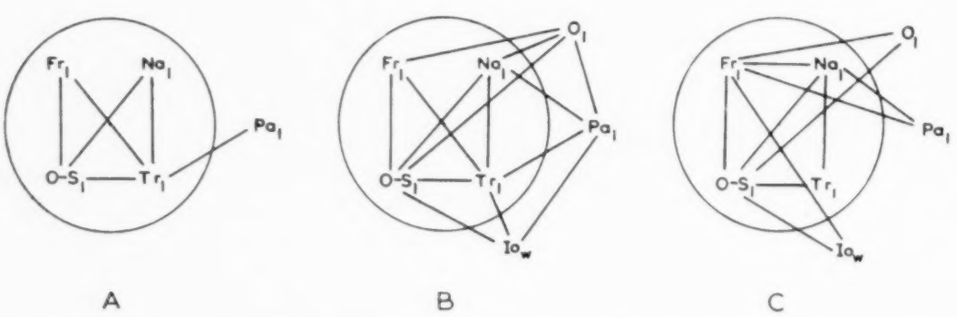

FIG. 1. ρF-groups in Species 1, A, Species 2, B, and Species 3, C. The connecting lines indicate correlations (ρ) attaining the arbitrarily chosen high standard of .95 (with statistical risk in a one tailed test of 0.5). All groups of ≥ 2 members are shown. The single F-group is circled. For abbreviations see pages 326 and 327.

one or more of the following: (1) Other F-groups may include these members. (2) There may be underlying developmental patterns that are not expressed in function. (3) There may be genetic linkage. These associated measures will be defined as bonded under the discussion of $F_{mast.}$

5. Sk_1 has been omitted from the groupings. The position of Sk_1 in the ρ-grouping and its effect on the correlation values of other pairs of measures is discussed later.

Further Analysis of the Masticatory Complex

The tentative masticatory complex members in the three species are all length measures. It seems reasonable to suppose that a factor common to all-over length of the skull might account for much of the correlation between any two of these measures, and that ρ-groups would be simplified if all correlation values were recalculated with Sk_1 held constant. This was done for Species 1 and Species 2. Unfortunately the sample size of Species 3 was too small to allow meaningful application of partial correlation techniques. The results of the analysis are shown in figure 2.

The arbitrary ρ value employed here was $\rho_{i_{min}} \neq 0$. Thus the ρ-group includes all pairs of measures whose correlations are not equal to zero. $F_{mast.}$ was again superimposed over the resulting ρ-groups. The change in ρ value from that used in the preceding consideration is based upon the following reasoning. The intercorrelation between any pair of measures is expressed as a numerical value. All measurements on the organism form a "closed" system in that each conceivably has some effect upon the correlation between all other pairs. If a certain measure is held constant, the absolute value of ρ between any pair may be either raised or lowered. Thus some concept of factors common to the pair and to the measure held constant can be gained. Sk_1, in particular, must have an important effect on the value of the correlation between many pairs. This was found to be the case using the arbitrary level of ρ as shown in figure 2.

Since Sk_1 is not in F, it was hoped that a clearer concept of the masticatory complex might be gained when Sk_1 was held constant. In Species 1 and Species 2, factors common to Sk_1 and to the masticatory complex apparently contribute greatly to the ρ values that bind the measures together. O_1 is now added to the ρ-group and the interrelationships among F members are changed in Species 1. In Species 2, the masticatory complex is notably simplified.

Partial correlation appeared to give meaningful results with Sk_1 held constant. The effects in Species 1 and Species 2 when other measures, not in $F_{mast.}$, are held constant in turn are shown in

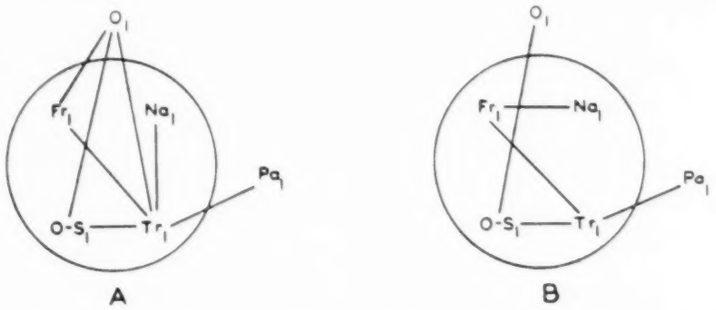

FIG. 2. Results of partial correlations with Sk_1 held constant in Species 1, A, and Species 2, B. The connecting lines indicate correlations (ρ) $\neq 0$. The single F-group is circled. For abbreviations see pages 326 and 327.

figure 3. A comparison of the effect of factors common to Pa_1 and the other measures on Species 1 and Species 2 with the corresponding ρ network in figure 1 shows that these effects differ in the two species. When Io_w and O_1 are held constant in turn there is relatively little breakdown from figure 1 in Species 2. In Species 1, however, the relationships are complicated and the number of bonds greatly increased over those shown in figure 1. Apparently factors involved in Io_w and many other measures operate independently on the members of a given pair of these measures. As a result the numerical expression of association of pairs of measures is in many instances increased when Io_w is held constant.

The "factors" alluded to in this section appear to vary in their influence from species to species. It therefore becomes interesting to speculate concerning the nature of the "factors." Differential genetic influence, function and environment all may operate to produce the types of modifications that have been noted. Further study of the interrelationships was undertaken in an attempt to throw light on this problem.

The Mechanism of Change

The morphology of an adult organism is the product of its growth patterns. An investigation of changes in relationships of the members of the masticatory com-

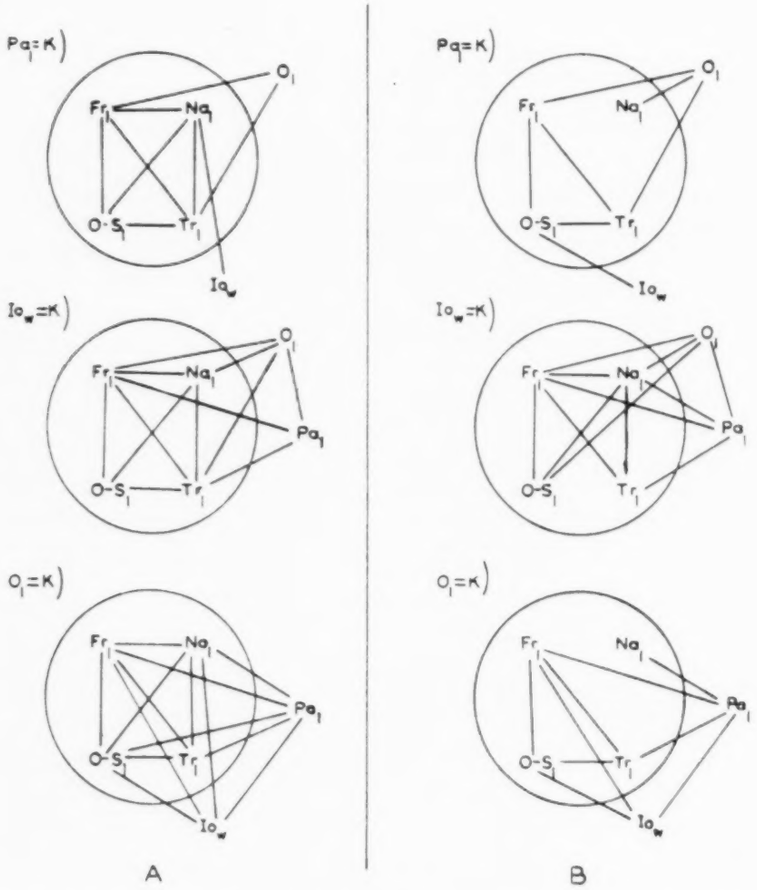

FIG. 3. Results of partial correlations holding constant in turn the measures not included in the masticatory complex in Species 1, A, and Species 2, B. K indicates measure held constant. Other symbols as in figure 2. For abbreviations see pages 326 and 327.

TABLE 2. *Comparison of regression patterns of Species 1 and Species 2.* a and b refer to differences of the constants in the equation Y = a + bX. Abbreviations as used earlier in the paper.

	$O\text{–}S_1$	Pa_1	O_1	Sk_1	Na_1	Fr_1	Tr_1	Io_w
$O\text{–}S_1$		a	same	a	a	same	same	b
Pa_1			a	same	same	same	a	b
O_1				same	same	same	same	b
Sk_1					same	same	same	same
Na_1						a	a	a
Fr_1							same	b
Tr_1								a
Io_w								

plex and related measures was therefore conducted by a comparison of bivariate regression lines between the species. Results are summarized in tables 2, 3 and 4.

Certain assumptions are made with respect to the comparisons of regression lines. It has been necessary to assume that both X and Y are normally distributed, which implies that the regression function is linear. In addition there are no *a priori* grounds for the choice of independent and dependent variables. There is an inherent difficulty in interpretation of any expression of the relationship between two biological measurements in terms of growth when the time factor is missing and acts as an uncontrolled variable. Two approaches have been studied by the writers, one being that of Huxley (1932) and the other that of Tessier (1948). The operational procedures followed in the present work were described in a previous paper by the writers (Olson and Miller, 1951).

The tables and figure 1 indicate the existence of similar differences between the $\rho F_{mast.}$ patterns and the differences apparent in the regressions. The analyses of the regressions suggest that an area between the orbits has been unstable during the evolution of the three species. This is based on the differences in slope (b) of the regression lines of Io_w with most of the other measures. The existence of this unstable area is confirmed by the loss of Io_w from the ρ-groups of Species 1. This relationship may be seen by comparing the $\rho F_{mast.}$ for Species 1 with that of Species 2 and Species 3 in figure 1, and comparing the regression lines of Species 1 and Species 2 in table 2. Additional support is given by negative evidence as shown by a comparison of $\rho F_{mast.}$ for Species 2 with that for Species 3 and a similar comparison of the regression tables. In summary, Species 2 and Species 3 are similar in terms of $\rho F_{mast.}$ and similar with respect to regression comparisons. Species 1, on the contrary, differs from Species 2 and Species 3 both in $\rho F_{mast.}$ and in lines of regression.

The appearance of differences in relative growth patterns in the interorbital area (Io_w) with respect to other parts of the skull seems to provide reason to expect a suite of other changes of varying degree that reflect modifications in the interorbital area. Inspection of the regression comparisons of Species 1 and Species 2 in table 2 shows a scatter of changes in initial growth constants (a). This is revealed to a lesser degree in the comparison of Species 1 with Species 3

TABLE 3. *Comparison of regression patterns of Species 1 and Species 3.* *, sample too small for meaningful comparison. Other symbols and abbreviations as in table 2.

	$O–S_1$	Pa_1	O_1	Sk_1	Na_1	Fr_1	Tr_1	Io_w
$O–S_1$		same	same	a	a	same	same	same
Pa_1			same	same	same	same	a	*
O_1				same	same	same	same	b
Sk_1					same	same	a	same
Na_1						same	same	same
Fr_1							same	same
Tr_1								a
Io_w								

in table 3. It should not be present to any marked degree in the comparison of Species 2 and Species 3 (table 4) and this is the case.

This evidence, plus that of the $\rho F_{mast.}$ patterns, gives a basis for speculation concerning the factors that underlie the evolutionary changes of the skulls of the three species. A genetic change that affected the relative growth patterns of the interorbital area with respect to the rest of the skull would in turn tend to affect various other developmental patterns and result in modification in the adult form. A morphological change of this type might affect various functional areas, such as the masticatory area. This change may be seen in figure 1, which shows that measures strongly bonded to F members in Species 2 and 3 are absent in Species 1.

THE MODES OF CHANGE

The differences between the three species have been documented and information concerning the mechanism of change has been given in the preceding sections.

TABLE 4. *Comparison of regression patterns of Species 2 and Species 3.* Symbols and abbreviations as in table 2.

	$O–S_1$	Pa_1	O_1	Sk_1	Na_1	Fr_1	Tr_1	Io_w
$O–S_1$		same	same	a	same	same	same	a
Pa_1			same	same	same	same	same	*
O_1				same	same	same	same	same
Sk_1					same	same	same	same
Na_1						same	same	same
Fr_1							same	same
Tr_1								same
Io_w								

The evolution of the three species is postulated to have taken place as follows:

1. Species 3 resembles the actual ancestral stock closely and has descended from it with little or no change in the skull. Minor genetic changes, perhaps random recombinations, produced within it a new genetic strain. Genetic isolation followed and the new strain came to occupy the environmental niche supplied by the margins of ponds and small lakes on the Permian delta. The genetic changes affected relative growth patterns and slightly modified the relationships of the members of $\rho F_{mast.}$ and their bondage to other measures. The principal change, however, at least as far as the skull is concerned, was a marked increase in the size of adults. This strain became Species 2.

2. A second new genetic strain arose from Species 3, the parent population. Perhaps this new strain was initiated or strongly influenced by a change in the genotype that produced lateral expansion of the maxillary and dentary field (in the sense of Butler, 1937) accompanied by the addition of rows of teeth roughly parallel to the original row of cheek teeth. Other genetic changes that may have altered certain relative growth patterns are most strikingly shown in the interorbital area. Modifications in masticatory function resulted from these changes. This strain occupied an environmental niche provided by the flood plains and divides of the delta and thus became genetically isolated. This new strain became Species 1.

The chain of events may be described as a series of steps from the following point of view. Change in function made possible the occupation of an environmental niche not occupied by the parent population. This modification is reflected in part by alteration of the membership and interrelationships of members of a ρF-group. The postulated mechanism was a change in relative growth patterns in a field that is genetically controlled and is part of a ρF complex. Less intimately related to patterns of relative growth, but, perhaps, influenced by the same or concurrent genetic changes are such characters as size of adults and patterns of dentition.

Evidence for this reasoning is as follows:

1. The environmental domain of Species 1 is believed to have been the flood plains of delta streams and divides between them. Specimens are found widely scattered in sandstones and clays of considerable lateral extent that are clearly of flood plain origin. In contrast, specimens are rarely encountered in typical stream and pond deposits. The flood plains deposits, in which Species 1 occurs, also contain remains of such typically terrestrial animals as *Dimetrodon*. They rarely yield aquatic genera. Frequency distributions based on length measurements suggest that seasonal phenomena were unimportant in deposition of the specimens of Species 1 (Olson and Miller, 1951).

2. The environmental domain of Species 2 appears to have been the margins, and perhaps the waters, of small lakes and ponds. Specimens usually occur in concentrations in lacustrine deposits. They occur rarely, if ever, in typical flood plains deposits and only as occasional scraps in channels. Only one questionable association of Species 1 and Species 2 has been observed by the senior author in eight seasons of field work. Such aquatic genera as *Diplocaulus* and partially aquatic genera as *Seymouria* are common associates. Terrestrial animals such as *Dimetrodon* also occur in the pond deposits, perhaps trapped while feeding. The sample of Species 2 shows some evidence of seasonal accumulation.

3. The environmental domain of Species 3 is not well understood, for the sample was obtained from deposits in Oklahoma that the writers have not studied. The known specimens occurred in red

sandstone and have come from a single concentration.

4. Inferred change in masticatory function is based on evidence of modification in size, dentition and the masticatory complex.

5. Partial correlation studies show the presence and effects of factors common to certain measures and to functional complexes. The influence of these factors varies from species to species.

The conclusion that Species 3 most closely resembles the actual parental stock is based on several lines of evidence. None is conclusive, but taken together they present a strong case. Stratigraphic and geographic relationships, paleoecology, morphology and evolutionary trends are all important evidence. The stratigraphic relationships are questionable so far as they pertain directly to the three species. Species 1 ranges from the Admiral formation of the Wichita group through the Clyde, Arroyo and Vale of the overlying Clear Fork group. Species 2 and Species 3 are known only from the Arroyo and Wellington formations respectively. These two appear to be time equivalents. Species 1 and Species 2 occur in the same formation whereas Species 3 was presumably geographically isolated.

Evolutionary patterns in general tend toward the production of larger species, although, of course, there are many exceptions. Thus it seems probable that small Species 3 may have been ancestral to the larger Species 2. It seems logical that a simple dentition, such as that of Species 2 or Species 3, represents the ancestral condition. This is to some extent supported by stratigraphic evidence in the case of other captorhinomorph reptiles. Members of this group known from deposits older than the Admiral formation of the early Permian appear to have single rows of teeth. *Cephalerpeton* (Gregory, 1948) and *Romeria* and *Protorthyris* (Price, 1937) are examples. A single row of maxillary and dentary teeth thus may represent the primitive condition. All known captorhinomorphs from post-Arroyo beds of Oklahoma and Texas, on the other hand, have multiple rows of teeth. *Labidosaurikos* from the Hennesey (Stovall, 1950) and at least three unnamed genera, recently obtained from the Vale, Choza and San Angelo formations by the senior author, are examples. Multiple rows of teeth appear to have been a rather late acquisition in the phylogeny of the group and to constitute a specialization.

Field evidence indicates that Species 1 and Species 2 were ecologically separated and occupied specific niches. The environment of Species 3, although poorly understood, probably was different from that of the other two. These conclusions as they bear on the problem of the ancestral population, however, are somewhat uncertain.

Species 1 clearly differs from Species 3 more than does Species 2. Species 1 might have been derived from Species 2 by continuation of certain of the changes that transformed Species 3 into Species 2 plus the initiation of other modifications, but the size factor renders this improbable. The nature of the masticatory complex, the dentition and adult size of each of the species suggest that the mode of population differentiation outlined in the opening paragraph of this section seems most reasonable. Geographical and ecological evidence does not appear to be contradictory and in part it supports this hypothesis.

Conclusions and Summary

The paleozoologist attempts to reconstruct events after they have happened. Recent advances in population genetics, biochemistry and other biological fields and the extensive body of knowledge accumulated in comparative anatomy are available for his use but must be applied by analogy. Application of the principle of uniformitarianism to animals of the past establishes neozoology as a powerful court of appeals for paleozoological the-

ory. This need not, however, be the only possible approach in the study of evolution of extinct groups at low taxonomic levels. Neozoological knowledge may be applied to the study of fossils in two ways: first as a guide in the development of hypotheses and second as a source of information to be tested in the light of paleozoological data independently gained. At the level of mega-evolution (Simpson, 1944) this has been done and much has been accomplished.

The writers have been concerned with evolutionary differentiation at a very low taxonomic level, where differences are small and most interpretations are not obvious. Standard methods fail to reveal many morphological differences and generally do not provide a basis for determining the factors involved in producing them. To study differentiation at this level the writers have investigated the interrelations of characters. A new concept, that of the ρF-complex derived from the study of measurements, has been introduced. Numerical interrelationships are expressed in terms of the correlation coefficients from which groupings, defined as ρ-groups, are obtained. Functional and/or developmental groupings, independently derived, are expressed as F-groups. The intersects of the ρ- and F-groups constitute ρF-patterns of the species or other taxonomic units involved.

It has been shown that changes in the ρF-patterns are intimately related to changes in patterns of relative growth and that the latter reflect the mechanism of change. The following presents the line of reasoning used to link inferred change in genotype to change in phenotype, which can be observed in fossils, and demonstrates the position and utility of the ρF-patterns and the relative growth patterns in the chain of events:

Given minor changes in gene complex:

1. The initial state of the organism is different from that of its parents.

2. During early growth, results of genetic changes become incorporated in the differentiating parts of the organism and the influence of these changes spreads as complexity of the organism increases.

3. The adult form is a product of relative growth patterns. The relative importance of initial ontogenetic change may be indirectly measured by noting the resulting change in adult morphology.

4. Morphological comparison of populations may be meaningfully expressed in terms of ρF-patterns.

5. The complementation of the concept of ρF-patterns and the concept of relative growth forms a basis for analysis of differentiation of small taxonomic units from a parent stock.

Mathematical Appendix

Consider n morphological quantitative characteristics and assume:

1. If $X_1, X_2, \ldots X_n$ are random variables corresponding to the n quantitative characteristics of a species, then $X_1, \ldots, X_n$ may be treated as if they follow a multivariate distribution. "ρ_{ij}" will denote the correlation coefficient between any pair of variables such as X_i and X_j.

2. Any subset of X's may or may not be functionally and/or developmentally related. Quantitative characteristics may be called measures in the sequel.

Definition: A ρ-group of the X's is any group, $X_{i_1}, X_{i_2}, \cdots, X_{i_k}$ such that:

(1) $|\rho_{i_m i_n}| \geqslant$ (an arbitrarily selected value) $m,n = 1, \ldots, k$.

(2) For any other X_j (i.e., $j = i_1, i_2, \ldots, i_k$) there exists at least one i_m $(m = 1, \ldots, k)$ such that $|\rho_{j i_m}| <$ (arbitrary value).

Thus (1) insures high intracorrelation in the subgroup and (2) insures that all highly correlated X's have been included.

It is clear that the ρ-groups may overlap and a given variable may be in more than one ρ-group.

Definition: An F-group of the X's is any group $X_{i_1}, \cdots, X_{i_n}$ in which all members are thought to be functionally or developmentally related. These groups

are chosen independently of ρ-groups on the basis of biological considerations.

Definition: A F-group of the X's is any group of the form $A\rho \bigcup A_F$ where:

(1) $A\rho$ is a ρ-group;
(2) A_F is an F-group;
(3) $A\rho \bigcap A_F \neq O$ (i.e. $A\rho$ and A_F have at least one common member).

Thus the grouping based on high intercorrelation and the grouping based on function or development must overlap to form a ρF-group.

The model consists of a number of ρ-groups of various sizes that form a network of measures. The links in this network are arbitrarily selected ρ values. Superimposed over this network is the F-group. ρF-groups formed in this way are clusters of measures thought to be appropriate for studying evolutionary change.

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THE ORIGIN OF THE ASTRAGALUS OF REPTILES

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INTRODUCTION

The structure of the tetrapod ankle holds considerable interest for the student of vertebrate history, and much has been written on the subject in the past century. In recent years the comprehensive and valuable study by Schaeffer (1941) has outlined effectively the history of the tetrapod ankle from the functional and morphologic point of view. With Schaeffer's results I am in general agreement, and it is the purpose of my paper to describe new paleontologic evidence which supplements and supports Schaeffer's conclusions concerning the origin of the reptilian tarsus and in particular the astragalar bone. For a review of past work on the tarsus and of concepts formulated, reference may be made to Schaeffer's account.

DISCUSSION

At present there is general agreement that the primitive reptilian tarsus was derived from an amphibian plan somewhat like that shown by the rhachitome, *Trematops* (fig. 1), in which there are 12 basic units—tibiale, intermedium, fibulare, proximal (4th) centrale, 3 distal (1st, 2nd, 3rd) centralia and 5 distal tarsalia. However, with respect to the transition from the amphibian to the reptilian tarsus (fig. 2) with its evolved astragalus there is no general agreement among morphologists as to what has happened to some of the proximal tarsalia, and in particular there is lack of agreement as to what units, if more than one, are involved in the formation of the astragalus. Upon the answer to this problem rests also the solution to other problems such as the origin of the mammalian navicular.

The tarsus of a primitive pelycosaur, of a captorhinid cotylosaur, or of a petrolacosaur, consists of a discoid calcaneum (= fibulare), an evolved "L"-shaped astragalus articulating distally with a median (1st) centrale and lateral (2nd) centrale, which may be fused, and a distal transverse row of five distal tarsalia. Schaeffer (1941, p. 428) concludes mainly from a review of embryological evidence, especially Holmgren (1933), that the origin of the astragalus is the result of a fusion of two or more bones of the amphibian complex, in particular the inter-

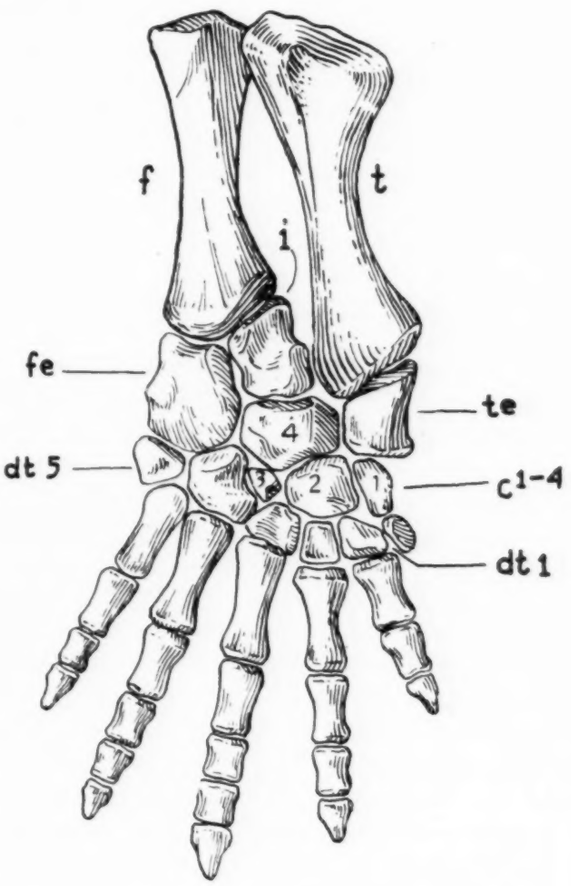

FIG. 1. Pes of *Trematops*, dorsal view; after Schaeffer, 1941.

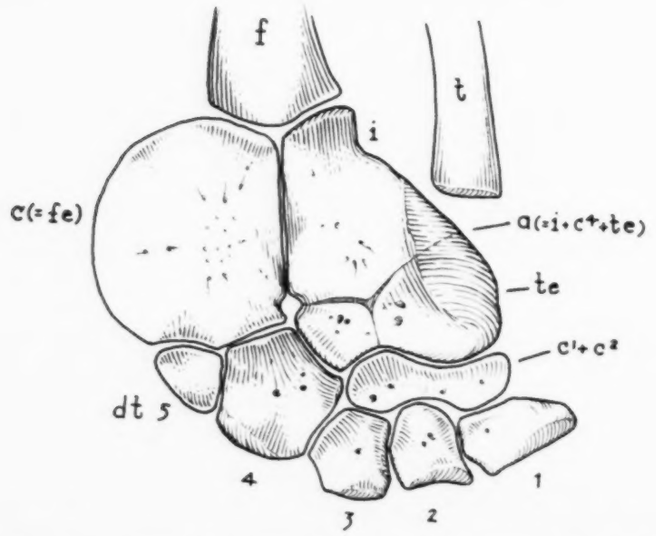

FIG. 2. Right tarsus of *Captorhinus*, × 4.5, dorsal view; composite based on K.U.M.N.H.[1] nos. 8964, 8965, 9783. Abbreviations: nf—nutritive foramen, f—fibula, t—tibia, a—astragalus, c—calcaneum, te—tibiale, i—intermedium, fe—fibulare, c^{1-4}—centralia, dt—distal tarsale.

medium, proximal centrale and *possibly* the tibiale. On the other hand, Romer (1931, 1940, 1945) and others believe that the tibiale was lost or displaced in reptiles, and the loss resulted in a shortening of the preaxial tarsal border of the primitive reptile thus facilitating an inward torsion of the pes, and in pelycosaurs a crurotarsal joint. Schaeffer (1941, p. 431) rightly observes that "a comparison of the *Seymouria* and *Labidosaurus* tarsi would seem to indicate that there has been no shortening of the inner border of the tarsus through the loss of the tibiale." Broom (1921) postulates that in the pelycosaur-therapsid-mammalian phylum the tibiale moved distad to become the navicular bone of mammals, a seemingly unlikely event in view of the fact that the "migration" had to take place in a constantly functioning tarsus and at a particularly critical locus in the locomotor mechanism of a terrestrial tetrapod.

As Schaeffer points out, the embryological evidence, although often difficult to interpret, indicates that the astragalus is probably a compound and possibly a tripartite structure, and he also points out that the paleontologic evidence has hitherto been neutral although the homology of the fibulare with calcaneum is clearly demonstrated by the position of the perforating foramen in the earliest reptiles.

Recently I have had the opportunity at the University of Kansas Museum of Natural History to study the remains of several individuals of a primitive Pennsylvanian reptile (Peabody, in press) from Kansas, *Petrolacosaurus kansensis*. Also, and of special interest, I have had the opportunity to study many remarkably preserved tarsal elements, some perfectly articulated, of a species of small *Captorhinus* found in fissure deposits of Lower Permian age near Fort Sill, Oklahoma. (Skeletal elements of the genus occur perfectly preserved and literally by the millions in the fissure deposits, and for the most part may be freed of the soft clay matrix simply by washing with water.) In both genera mentioned the tarsal elements are fully ossified in the adult; the general osteology and the geologic occurrence indicate a purely terrestrial habitat.

In both genera there is clear evidence

[1] K.U.M.N.H.—Kansas University Museum of Natural History.

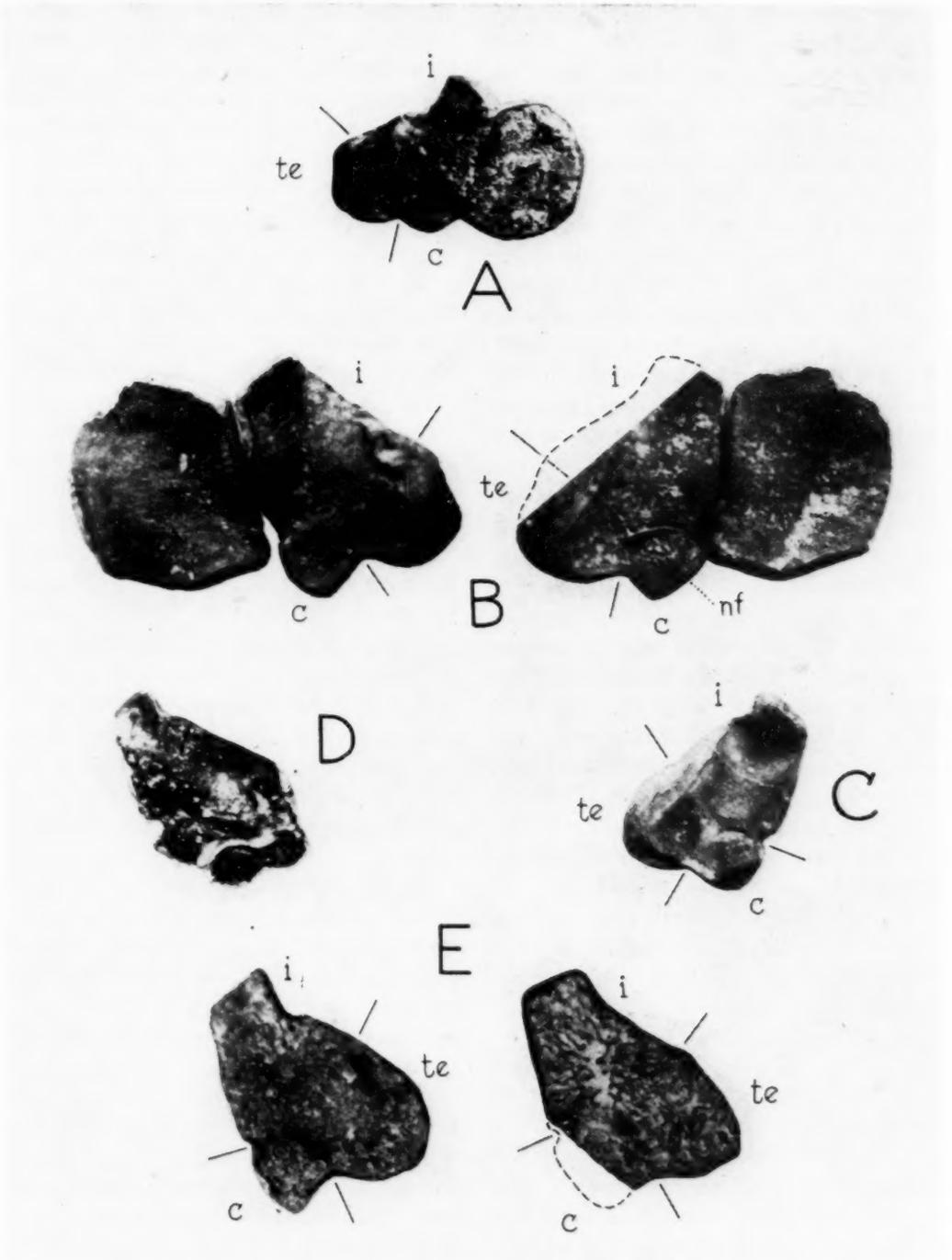

PLATE I. Unretouched photographs of selected K.U.M.N.H. specimens showing tripartite structure of the astragalus of *Captorhinus*, × 3.5. (See figure 2 for abbreviations.)

A. Left astragalus with articulated calcaneum, no. 9782, showing open sutures on dorsal surface.

B. Left astragalus with associated calcaneum, no. 9783, showing (on right) open sutures on dorsal surface, and (on left) fusion ridges on ventral surface of astragalus.

C. Left astragalus, no. 9785, showing light colored fusion ridges on dorsal surface (thin white line across neck of intermedium is an accidental crack).

D. Right astragalus and "navicular" from nearly complete pes, no. 8964.

E. Two astragali, no. 9784, sectioned parallel to dorsal surface, showing tripartite spongiosum, and definite sutures between centrale and other two components of the astragalus.

that the astragalus is a composite structure. An incompletely ossified but articulated tarsus of a young individual of *Petrolacosaurus* (no. 1426) has an astragalus showing a laterodistal area structurally separate but partly ankylosed to the main body of the astragalus and clearly corresponding to the proximal centrale of *Trematops*. The mediodistal part of the astragalus (which is broken parallel to the dorsal surface) shows faintly a separate nucleus of spongiosum suggesting the tibiale. In an adult specimen (no. 1424) there is a deep notch in the distal border of the astragalus at the same position as the notch described below for *Captorhinus* and in the latter marking the suture between a definitive tibiale and centrale.

Thirty-five adult astragali of *Captorhinus* at hand demonstrate beyond a doubt that the astragalus of this primitive reptile is a tripartite bone consisting of an intermedium, proximal centrale, and a robust tibiale which contributes to approximately two-thirds of the tibial facet. In each of the diminutive astragali there is a definite indication on the dorsal surface of tripartite structure in the form of fusion ridges which are slightly higher and lighter in color than surrounding bone (Pl. IC), or this is indicated in a few specimens (apparently adult) by lack of perichondral bone along dorsal sutures (Pl. IA, B). On the more irregular ventral surface of the astragalus the sutures tend to be more obscure, but in astragali showing open sutures on the dorsal surface there are closed sutures plainly evident on the ventral surface (Pl. IB, left). Nutritive foramina on the dorsal surface of the astragalus are in three groups independently indicative of tripartite structure, and faint striae radiate from each group of foramina. Two astragali (Pl. IE) showing relatively slight surface indication of tripartite structure when sectioned parallel to the dorsal surface show traces of sutures, most strongly between proximal centrale and intermedium, and also definitely three nuclei in the spongiosum. Centers of these nuclei correspond to the centers of the three groups of nutritive foramina appearing on the dorsal surface. Of the 35 specimens, one astragalus found covered with encrusting matrix lacks the tibiale which broke away cleanly before or during burial in the fissure deposit. Two astragali washed free from the matrix lack the proximal centrale, also broken away cleanly at the suture. Finally, one isolated intermedium, perfectly preserved, demonstrates that all three components of the astragalus may become disarticulated, so weak is their union. All evidence considered, the suture between tibiale and intermedium is least well-defined and almost invisible on the face of the tibial facet. This last is to be expected on such a critical articular surface. The sutures between centrale and intermedium and between centrale and tibiale are the most clearly defined, that is to say, the weakest, structurally speaking. No correlation seems to exist between the size of the astragalus and the degree of fusion of the component parts.

It is noteworthy that the perforating foramen occurs, as expected, at the junction of intermedium, centrale and calcaneum, and the distal junction of the centrale with the tibiale is marked by a prominent, angular notch in the distal border of the astragalus.

Contrasting with the clearly composite astragalus is the calcaneum, also represented by many specimens. It shows clearly by its surface contours, nutritive foramina, and by internal structure that only a single unit is involved. This substantiates the evidence usually employed in fossil specimens to demonstrate homology of the calcaneum with the amphibian fibulare.

Granted that the tarsus of *Captorhinus* clearly demonstrates that the amphibian tibiale, intermedium, proximal centrale and fibulare are represented by the as-

tragalus and calcaneum, then the homologies of more distal elements became clear. The angular "navicular" with its dumbbell shape and fitting precisely into the deeply notched border of the astragalus (Pl. ID) seems to represent a fusion of two centralia, the median and lateral centralia of primitive pelycosaurs. In 21 available specimens of the tiny "navicular," 6 suggest duplex structure in the grouping of nutritive foramina on the dorsal and ventral surface and also by a proximodistal line of color, lighter than surrounding bone, crossing the neck of the "dumbbell." Also the dorsal and ventral surfaces each show two shallow depressions separated by a high (topographic) area at the color line on the neck of the "dumbbell." Spatial relationship of the duplex "navicular" to neighboring elements suggests a natural, non-serial arrangement of originally separate median and lateral centralia, originally separate tibiale and proximal centrale, and the distal tarsalia. Two transverse sections made from "naviculars" are only faintly suggestive of a duplex structure of the spongiosum. In the tarsus of *Labidosaurus* studied by Schaeffer a proximodistal shortening of proximal elements of the tarsus has occurred; the "navicular" is especially compressed, and its duplex structure, if real, is not apparent in its dorsal outline.

It is suggested here that the tarsus of *Captorhinus* as now known is more nearly ideal for the primitive reptilian plan than is the tarsus of *Labidosaurus* as suggested by Schaeffer. The tarsus of primitive pelycosaurs, and of *Petrolacosaurus* and *Captorhinus*, lacks the proximodistal shortening seen in *Labidosaurus* and in larger cotylosaurs, and, moreover, has the overall proportions of the amphibian tarsus. It is possible that the tarsus of the primitive pelycosaur with its separate median and lateral centralia may prove to be closest to the primitive reptilian pattern.

The plan of the captorhinid tarsus is easily derived from the amphibian plan shown by *Trematops*. Indeed, if the astragalus and "navicular" be separated into their five component parts, and if the median corner of the oversize fourth distal tarsale be imagined as representing the third centrale, then we have very nearly the plan of the tarsus in *Trematops* except for the fixed articulation between intermedium, tibiale and proximal centrale, and the specialized tibiale facet. Thus, there is demonstrated in a primitive reptilian tarsus a relatively simple fusion of several amphibian elements which resulted probably as an adjustment to stresses involved in the formation of a specialized tibiotarsal joint. Such a joint would tend to eliminate torsion of the anteriorly directed pes while it was in contact with the ground.

The close similarity of captorhinid and pelycosaurian tarsi leaves little doubt that the astragalus of the pelycosaur is also tripartite approximately in the manner described for *Captorhinus*. If this be granted, then the navicular of therapsids and of mammals cannot be a displaced tibiale. Rather the navicular represents the lateral (2nd) centrale or possibly the fused median (1st) and lateral centralia found separated in primitive pelycosaurs. Also, the free movement of tibia on astragalus among pelycosaurs as described by Romer (1940) could not have been gained through loss of the tibiale but by construction of a convex, oblique facet formed only partly by the intermedium and mostly by a robust tibiale.

Summary and Conclusion

The tarsus of *Captorhinus* from the early Permian is the most primitive of known reptiles in which there is an evolved astragalus, with the possible exception of the tarsus of *Petrolacosaurus* from the late Pennsylvanian. Discounting the probable fusion of the median and lateral centralia, separate in some pelycosaurs, the tarsal plan of *Captorhinus* with

its clearly tripartite astragalus is exceedingly close to a theoretical transition from an amphibian plan, as shown by *Trematops,* to the reptilian plan. Thus, Schaeffer's conclusion from embryologic evidence that the reptilian astragalus is possibly tripartite is fully substantiated by paleontologic evidence. Because the primitive astragalus includes the proximal centrale and the tibiale it seems reasonable to homologize the mammalian and therapsid navicular with the lateral or lateral and median centralia of pelycosaurs.

ACKNOWLEDGMENT

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CONVERGENT EVOLUTION: THE JAWS OF *HESPERORNIS* AND THE MOSASAURS

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INTRODUCTION

A striking example of convergence, the evolution of similar structures from different antecedent body plans by unrelated organisms, is provided by the comparison of the lower jaws of the Cretaceous toothed bird, *Hesperornis,* and those of the giant marine lizards known as mosasaurs, whose skeletons are entombed within the same strata. O. C. Marsh, the discoverer of *Hesperornis,* himself briefly noted the presence of an intramandibular joint in its jaw (1880, p. 11), but his interest in the retention of teeth and the supposedly primitive brain (cf., Edinger, 1951) of this bird led him to neglect further consideration of this feature. Elsewhere among tetrapods a splenio-angular articulation is known only in the mosasaurs in which it has been described in detail by Williston (1898, pp. 130–134).

The structural similarities of the mandibles of mosasaurs and *Hesperornis* are so great that it is hard to realize that they have arisen independently from rather dissimilar types of reptilian jaws. Yet such is clearly the case, for *Hesperornis* was a bird, derived from the reptilian Subclass Archosauria, whereas mosasaurs (fig. 6) are modified lizards [Subclass Lepidosauria] close to the living *Varanus* in their basic structure and undoubtedly derived either from the early Varanidae or their immediate precursors. Besides the distinctive mandibular joint the mosasaurs and *Hesperornis* show similarities in several other features, all of which may be related to their aquatic habitat and presumably piscivorous diet. Their convergence is thus adaptive and typical of that phenomenon.

This discussion is a by-product of an investigation of the jaws which Marsh attributed to another Cretaceous bird, *Ichthyornis.* Evidence is presented elsewhere which shows that these jaws probably did not belong with that bird skeleton but are actually young mosasaur jaws which were washed into the same deposit with bird bones of similar size. Routine comparison with *Hesperornis,* the only other Cretaceous bird sufficiently well known for comparison, brought the convergent condition mentioned above to light.

The present report is based upon detailed study of the lower jaws of *Hesperornis regalis* Marsh, Yale Peabody Museum No. 1206, and of *Hesperornis gracilis* [1] Marsh, Kansas University Museum of Natural History No. 2287, which to the best of my knowledge are the only extant specimens of these birds in which skull and mandible are preserved.

In the course of this study I have received valued advice and much encouragement from many colleagues, particularly Dr. Tilly Edinger, Dr. Hildegarde Howard, Dr. S. Dillon Ripley, and Dr. Alexander Wetmore. The illustrations were prepared by Miss Shirley Glaser.

HESPERORNIS

The large, toothed diving bird of the Cretaceous, *Hesperornis regalis* [2] Marsh

[1] Lucas (1903, p. 552) placed this species in a distinct genus, *Hargeria,* on the basis of the form of its quadrate, short nasal processes, and proportions of the femur. Comparison of his illustrations of *H. gracilis* with the type of *H. regalis* indicates that the differences are less than would be believed from Marsh's illustrations, and the generic separation of these species seems unwarranted.

[2] Several other described species are doubtfully distinct and closely similar in their main adaptations.

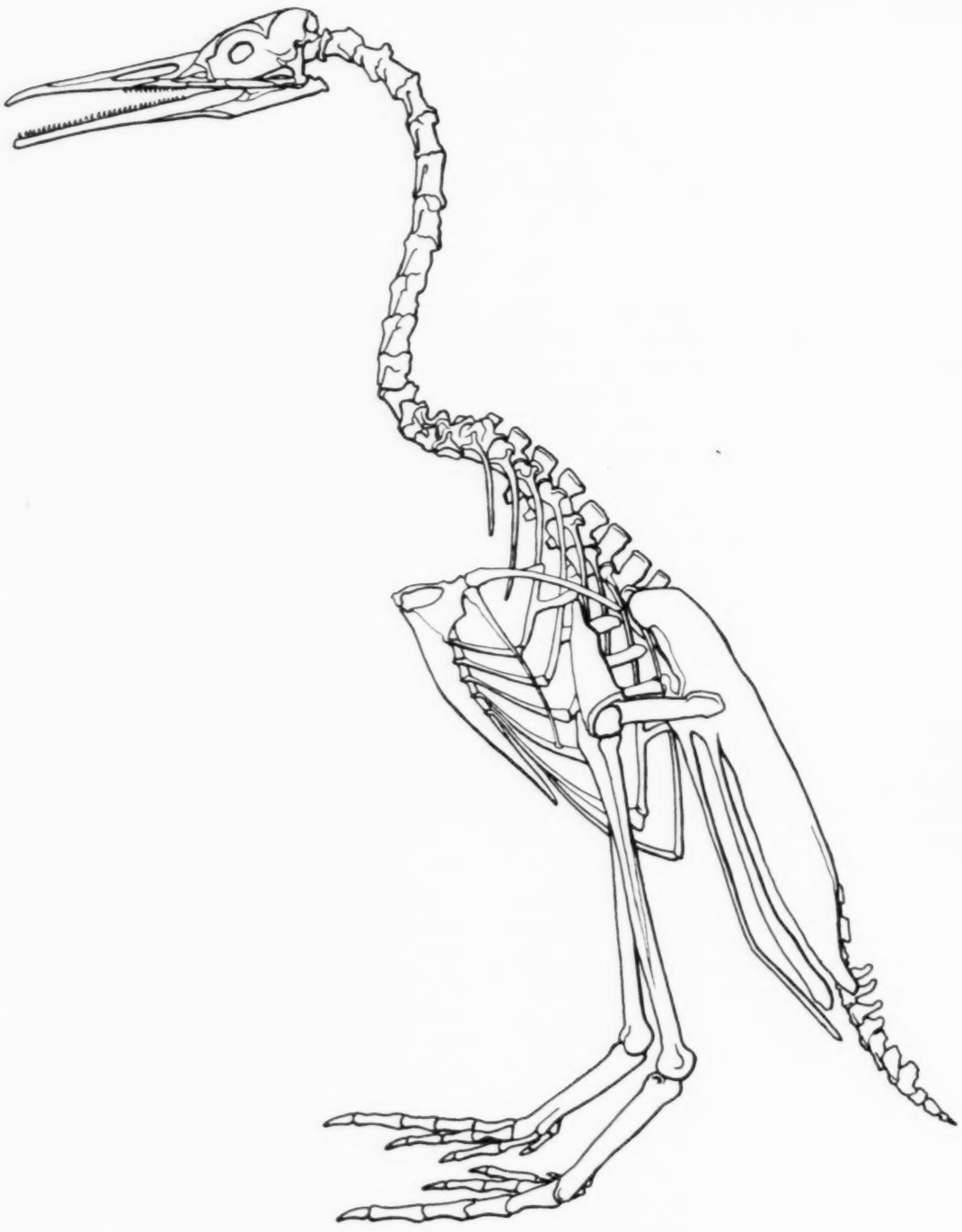

FIG. 1. *Hesperornis regalis* Marsh. Reconstructed skeleton of Cretaceous toothed diving bird. After Marsh, × 1/6.

(fig. 1), was about five feet in length and may be briefly characterized as possessing a fairly long beak, slightly recurved at the tip, a long neck, a streamlined body totally lacking external wings, and powerfully developed swimming feet. The skull shows many resemblances to those of the Podicipitidae,[3] and the specializations of femur, tibia and patella, and metatarsus are similar to but even more

[3] *Gavia* is used for the loons and *Podiceps* for grebes throughout this article.

extreme than in that family.[4] Detailed descriptions of these adaptive similarities may be found in the works of D'Arcy Thompson (1890) and Heilmann (1927, pp. 42–50). They show that like the living *Podiceps, Hesperornis* was a diving bird, at home in the water but, in the opinion of Lucas (1903, p. 551), Heilmann (1927, p. 50), and Wetmore (1929, p. 381), unable to walk on land. Marsh regarded it as a ratite, because of its unkeeled sternum, but Thompson, Shufeldt, and Lucas have all shown that the skull lacks distinctive characters of any of the "ratites." Lucas (*loc. cit.*) and Stolpe (1935, p. 126) regard the resemblances to grebes and loons as adaptive structures connected with similarity of habits and not necessarily significant of phyletic relationship.

The skull of *Hesperornis* is known from three fragmentary specimens: the dissociated and fragmentary type of *H. regalis*, Y. P. M. 1206; the occiput of Y. P. M. 1207;[5] and, by far the best, the specimen of *H. gracilis*, K. U. M. N. H. 2287.[6] From these materials the paper reconstructions and models illustrated in the literature have been prepared. As mentioned above, there are many resemblances to the skull of *Gavia* and also to that of *Phalacrocorax*, but two important features stand in contrast to these living birds: first, the presence of teeth on the maxillary and dentary bones, and second, the lack of bony symphysis of the lower jaws and presence of a transverse joint between splenial and angular bones. These structures form the subject of this discussion.

The upper beak is long and slightly downcurved at the tip, more so than in gannets (*Sula*) but less than in gulls (*Larus*) and much less than in cormorants (*Phalacrocorax*). Teeth were present only in the maxillary, toward the rear of the mouth gape, and the premaxillaries were evidently sheathed by a horny beak as in modern birds. The culmen probably was more strongly downcurved than the premaxillary itself, as in recent cormorants and gulls.

As restored by Marsh, the mandible of *H. regalis* was 257 mm. (10 in.) long; that of *H. gracilis*, restored by Miss Glaser, is about 208 mm. (8¼ in.). The two halves of the lower jaw were separate, or only ligamentously united at the tip. This feature contrasts sharply with all recent birds, in which the rami of the jaws are invariably fused together at the symphysis. It is one of the convergent anatomical resemblances to mosasaurs, which also lacked any symphysis of the jaws. Among living tetrapods the closest analogy is found among serpents, which also lack this symphysis and are thus enabled to expand the mouth tremendously for swallowing their prey, and also to force bulky prey down their throats by alternate movements of the two halves of the jaw. As will be shown, somewhat similar feeding habits may be postulated for *Hesperornis*.

Long, slender, but relatively massive, blunt-tipped dentaries bore deep grooves along the oral margin for insertion of teeth. Marsh also noted the presence of a lateral groove on the posterior part of the dentary which he suggested might have received the points of the maxillary teeth (1880, p. 11, cf., *ibid.*, Pl. I, fig. 3). Perhaps this is so; the structure is poorly preserved, and not dissimilar to grooves on the dentaries of modern birds for attachment of the horny beak.

None of the specimens preserve the posterior end of the dentary, but it is clear from the form of the splenial that it did not extend behind that element ventrally, and probably did not at all. The splenial is triangular bone, rounded to form the lower edge of the jaw at its ventral margin, rising as a thin plate along the inner surface of the jaw beside the posterior half of the dentary. At its

[4] Stolpe (1935) has shown that *Hesperornis* is more like *Podiceps cristatus* than *Gavia* ["*Colymbus*"] *arctica* in foot structure.

[5] Y.P.M.—Yale Peabody Museum.

[6] K.U.M.P.—Kansas University Museum of Natural History.

posterior end there is a pronounced projection of the lower margin, and a sloping hollow cylindrical facet for articulation with the angular (fig. 3, B and C).

The posterior section of the jaw, forming about two-fifths of its entire length, consists of the usual angular, surangular, articular and prearticular bones, the coronoid being absent as in all birds. There is no trace of a mandibular foramen, though the angular and surangular merely overlap without a suture for a short distance in front of the articular cotylus.

Of these elements the angular may be considered first. It forms the retroarticular process and extends forward along the lower edge of the mandible, its upper edge overlapped laterally by the surangular. Anteriorly it increases in height and thickens somewhat, and is terminated in a somewhat roughened, hemicylindrical surface which inclines forward and upward at an angle of 55° to its lower margin. (fig. 3A). This surface fits somewhat imperfectly with the concavity at the posterior end of the splenial; quite probably both surfaces were covered in life with a smooth layer of cartilage such as occurs in all diarthroses. The joint so formed permits a rotational motion of the anterior and posterior sections of the mandible on an oblique axis so that outward bowing of the intramandibular joint would be accompanied by an outward twisting of the tooth row and an inward rotation of the coronoid region.

Part of a slender, elongate prearticular bone is preserved in *H. regalis,* but the relations of this element to the remainder of the jaw are in no way indicated. Marsh's Plate I, figure 4, does not clearly show whether the element tapering posteriorly to a point along the upper part of the inner surface of the surangular was regarded as a projection of the dentary or the prearticular bone. This tapering element resembles the anterior end of the prearticular of the loon, *Gavia immer,* or cranes (Ardeidae) and in figure 2 it has been restored in an analogous position. The posterior end of the prearticular is fused to the dorsal edge of the angular in recent birds; a section is broken from the angular in all *Hesperornis* specimens at about this point so the relationship of these bones cannot be determined.

The prearticular undoubtedly spanned the intramandibular joint as did that of mosasaurs, and as in those reptiles served as a spring-leaf to help restore the jaw to normal position after distortion.

The surangular bears a moderate coronoid process, similar to that of cormorants, upon its dorsal border. Its anterior end is not preserved in any of the specimens, but it is reasonably assumed to have reached the dentary and perhaps slightly interdigitated with it as in many modern water birds.

The articular of *Hesperornis* is a small element confined largely to the region of the cotylus, of which it forms the major

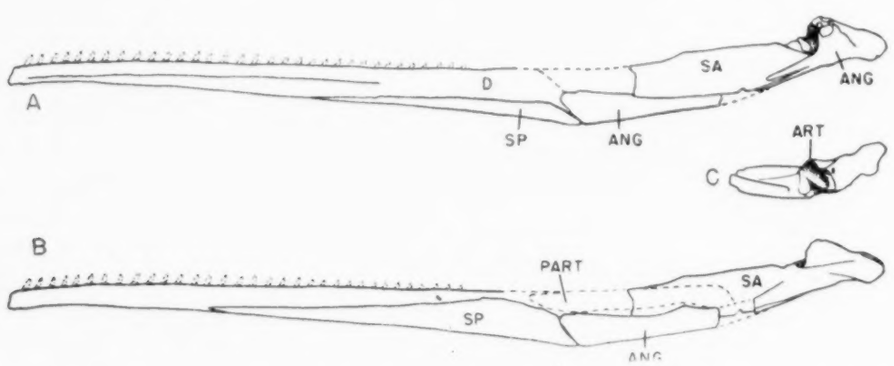

FIG. 2. Reconstruction of the lower jaw of *Hesperornis,* × ½. A, lateral view; B, medial view; C, superior view of articular cotylus. ANG angular; ART articular; D dentary; PART prearticular; SA surangular; SP splenial.

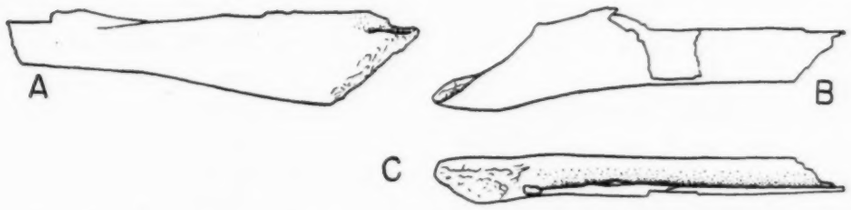

FIG. 3. Splenioangular articulation of *Hesperornis*. A, anterior portion of angular, medial side; B, medial; and C, superior aspects of splenial. *H. regalis* Marsh. Y. P. M. 1206. ×1.

portion. The cotylus resembles that of modern birds in its division into anterolateral and posteromedial sections, but it is simpler in construction. There is a somewhat oblique, elongate concave facet on the articular for the inner condyle of the quadrate. This is separated by a ridge from the lateral facet, which extends partly onto the surangular bone. Unlike the loon (*Gavia*), which among modern birds approaches it most closely in this region, there is no separation of posterior facet into two parts by a deeper concavity for the posteromedian quadrate condyle.

The teeth of *Hesperornis* were described in considerable detail by Marsh (1880, pp. 13–16). He records the presence of 14 in the maxillary and 33 in the dentary, figures which may well be correct but which I have not been able to verify satisfactorily. The crowns are somewhat curved, and sharp edged although not thin, and rise from swollen bony bases not unlike those of mosasaurs, ichthyosaurs, and plesiosaurs. The teeth were implanted in deep elongate grooves on each bone, not in separate alveoli.

In summary, the important features of the jaws of *Hesperornis* are:

1. Overall proportions and form most similar to those of the mandible of *Ardea*, except that the dentaries are slightly shorter relative to posterior moiety, and that the coronoid process is somewhat more anterior than in that genus.

2. Form of articular cotylus, and relations of articular and prearticular like those of *Gavia*, except that posterior cotylar groove is undivided.

3. Dentaries bearing recurved, pointed teeth with swollen bases which are set in an elongate alveolar groove.

4. An oblique, cylindrical articulation between angular and splenial bones, evidently accompanied by some interleaving between dentary, surangular, and prearticular to form a hinge whose motion was restricted by a spring.

5. Anterior ends of the dentaries not united by a bony symphysis, but free of one another or only ligamentously bound together.

MOSASAURS

In the Upper Cretaceous seas lived numerous marine lizards, closely related to the living monitors (Varanidae), but highly modified for aquatic life. Mosasaurs attained extreme lengths of 35 feet, though most known specimens are shorter; six feet is about the smallest known. Upon the fundamental structural plan of lizards, are superimposed these modifications for swimming: first, marked shortening and broadening of the bones of the arms and legs, flattening and reduction of mobility of the carpus and tarsus, and elongation of the phalanges accompanied by hyperphalangy and webbed digits to form efficient paddles; and second, compression of the tail to form a swimming organ, particularly in the genera *Clidastes* and *Mosasaurus* in which the neural spines of the subterminal caudal vertebrae are elongated.

Mosasaur skulls for the most part closely resemble that of *Varanus*, but their quadrates are modified to support the tympanic membrane, presumably an

adaptation to withstanding the large pressure changes encountered in diving. The lower jaws are remarkable for the absence of intermandibular symphysis, and for the development of an intramandibular articulation between splenial and angular.

Without entering into full description of the mandible, which has been given by Williston (1898, pp. 130–134) the details of the intramandibular joint may be noted. The splenial has much the same form as in *Hesperornis,* but the articular facet at its posterior end is smaller, nearly equidimensional, at the ventral edge (fig. 5A). It consists of a ventral concave pit, above which the facet is convex and nearly vertical on the outside, sloping off to a slightly concave surface which slopes forward a trifle on the inside. The facet is less than one-quarter the depth of the jaw in height, in contrast to that of *Hesperornis,* in which it extends fully half the total depth.

The angular is similarly enlarged at its anterior end and shaped into a facet which fits that of the splenial; that is, it has a marked ventral convexity, a concavity above it laterally and a forwardly projecting inner process (fig. 5B). It may be noted that the angular of mosasaurs, like that of lizards, is a small element confined to the ventral edge of the jaw anterior to the cotylus. It does not extend back to form the angle of the jaw.

In the mosasaur jaw, the anterior end of the prearticular is an extremely thin sheet of bone which extends forward medial to the surangular, crosses the gap between that bone and the dentary, and terminates between the posterior ends of the dentary and splenial. Posteriorly it extends backward, forming the ventral margin of the jaw and uniting with the articular to form the retroarticular process.

Surangular and coronoid both end rather abruptly just above the splenio-angular articulation, without meeting the dentary in suture. Thus the intramandibular articulation is spanned by the prearticular alone.

The articulation of the lower jaw with the quadrate in mosasaurs is a simple transverse concave facet, formed by the articular posteriorly and medially, by the surangular antero-externally (fig. 5C). It corresponds with the simple quadrate condyle and is closely similar to that in lizards. The proximal end of the quadrate, of course, was movably articulated with the skull.

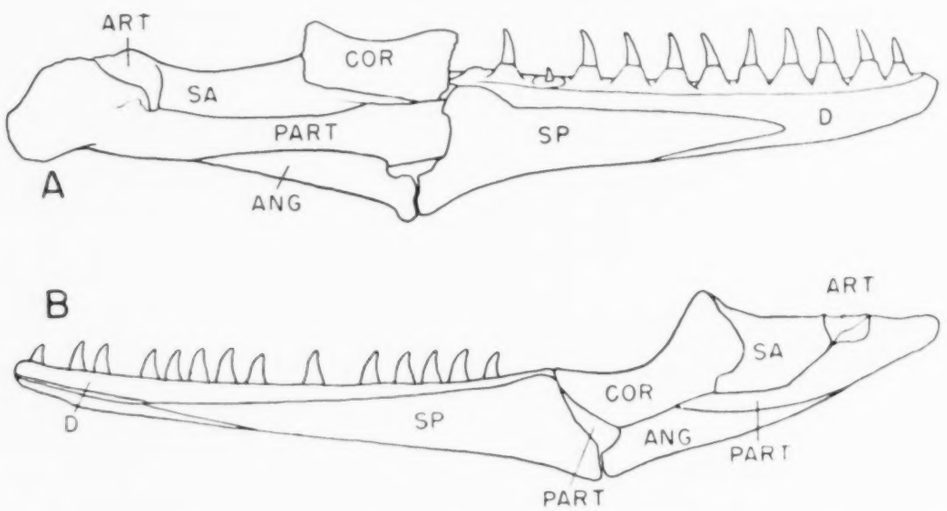

FIG. 4. A. *Platycarpus coryphaeus* Cope, × ⅕. B. *Clidastes tortor* Cope, × ⅐. Medial views of mosasaur jaws showing relationships of various bones and enlarged bases of teeth. Note prearticular spanning intramandibular joint and ventral position of the articulation between splenial and angular. ANG angular; ART articular; C coronoid; D dentary; PART prearticular; SP splenial. Adapted from Williston.

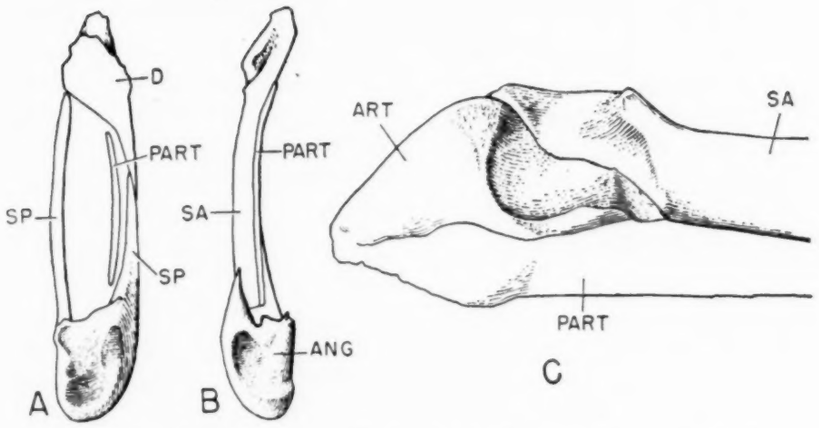

FIG. 5. A and B. Intramandibular joint of *Platycarpus* sp. A. Posterior view of splenial and dentary; B. Anterior view of angular, etc. C. Articular region to show form of cotylus of mosasaur jaw. All × ½.

The mechanism of the intramandibular joint of mosasaurs would have admitted considerable lateral and, according to Williston (1898, p. 130), slight vertical movements. There is no evidence in it of the peculiar rotation which must have accompanied movements of the jaw of *Hesperornis*.

Mosasaur teeth remain to be mentioned. They are conical, backward curved at the tip, provided with cutting edges, and have greatly swollen bony bases which are inserted in large alveoli in the jaw bones. Successional teeth appeared below, in regular sequence, and as they developed the osseous base of the functional tooth was eroded until it fell out and was replaced.

THE CONVERGENT FEATURES

Although they may now be obvious to the reader of the previous sections, the convergent features between the Cretaceous toothed diving bird *Hesperornis* and the Cretaceous marine lizards or mosasaurs are again summarized:

1. Marked modification for swimming in body form and limb structure; details of these modifications are quite different, for the fundamental body plans of birds and lizards are dissimilar and lend themselves to different types of progression through the water. The mosasaur swam mainly by lateral undulations of its body and tail; the latter organ was long, compressed, and at least in some genera vertically expanded. Feet were of secondary importance, and may be compared in structure and function with the "flippers" of a porpoise or whale, though posterior as well as anterior limbs were so modified.

Birds on the other hand, have short rigid bodies; all members of the Class which have become swimmers have modified the appendages for propulsion through the water. Most have developed webbed feet and appropriate musculature and limb configuration to operate these as oars or paddles; loons, grebes, and cormorants possess this adaptation in the highest degree. A few, the penguins and auks, have modified their wings for swimming, or as has been aptly stated "flying beneath the water." *Hesperornis,* being wingless, of necessity falls within the former group. Its hind limbs were so far modified for swimming that, like those of the loon, they were practically useless for progression on land. Full details of these adaptations are contained in Heilmann's account, and Stolpe has shown notable resemblances to grebes. There is no particular structural similarity to the limbs of mosasaurs beyond the development of webbed toes.

2. Recurved pointed teeth with swollen bony bases. This type of tooth was not

FIG. 6. *Clidastes velox* (Marsh). A small mosasaur, length about 10 feet. Redrawn from Williston.

characteristic of the ancestral stocks of either birds or mosasaurs, much less of their remote common ancestor. Somewhat similarly enlarged roots are found on ichthyosaur teeth. Plesiosaurs, the other major group of piscivorous aquatic reptiles, show no sudden swelling at the base of their otherwise somewhat similar conical teeth. Nevertheless this type of tooth is confined to aquatic reptiles and may be regarded as an aquatic adaptation of unknown significance, possibly related to piscivorous habits.

3. Lower jaw with transverse articulation between splenial and angular bones. This structure is unique in these two families. It is mechanically related to number 4.

4. Absence of bony symphysis of the rami of the two jaws.

Both *Hesperornis* and the mosasaurs are reasonably inferred to have been fish-eaters. The sharp pointed, recurved teeth of these animals are well suited for holding such lubricous prey. Independent anteroposterior movements of the rami of the jaws are used by snakes in forcing large food masses down the throat. Cope (1869, p. 216) considered this the probable mode of feeding of mosasaurs, but Williston (1898, pp. 212–213) has shown that movements of the quadrate must have been extremely limited, and suggested, instead, that mosasaurs forced their prey down the throat by lateral bending of the jaws at the transverse joint, the teeth releasing as the jaws sprang back into shape after the upper teeth had engaged the food mass. Recurved palatal teeth, which are well developed in both snakes and mosasaurs, are an important adjunct to such a feeding mechanism. *Hesperornis* lacks palatal teeth, but the posterior maxillary teeth and recurved tip of the beak served the same function of holding the prey while the jaws were being extended. The movable avian quadrate permitted alternate movements of the jaws, to a lesser extent than in snakes, of course, but probably as much as in mosasaurs.

Certain differences between *Hesperornis* and mosasaurs should be emphasized in evaluating the degree of convergence between these animals. This has already been done for the locomotor organs; in the jaws the following points of difference appear:

1. Difference in mode of implantation of the teeth, which are in individual alveoli in mosasaurs, but lie in a common groove in *Hesperornis*.
2. Difference in details of the intramandibular articulation with resultant differences in type of motion possible at that joint.
3. Differences in the form and orientation of the articular cotylus.
4. Differences in the arrangement of the bones in the posterior part of the jaw, notably the relative extent of the angular and prearticular, and presence or absence of the coronoid.

The first, third, and fourth of these are all clearly the result of differing heritage (as are the differences in locomotor organs).

The differences in detail of the intramandibular joint are as characteristic of convergence as are the similarities involved. Convergence implies that mechanically similar structures have evolved from diverse basic materials, and convergence does not lead to identity of form. Simpson has written of the "opportunism of evolution" . . . "that what can happen usually does happen; changes occur as they may and not as would be hypothetically best; and the course of evolution follows opportunity rather than plan" (1949, p. 160). "Evolution works on the materials at hand: . . . The materials are the results of earlier adaptations plus random additions and the orienting factor in change is adaptation to new opportunities" (*ibid.*, pp. 164–165). Such has been the history which led to these two types of animals. Ancestors of the mosasaurs, land-dwelling lizards, took to the sea and eventually became highly modified for aquatic life. These modifications included development of webbed, paddle-like flippers from the feet, a compressed swimming tail, and more streamlined body than that of terrestrial lizards. The streptostylic lizard skull became further modified for grasping and swallowing large fishes by loss of the bony symphysis of the jaws and consequent possibilities for independent motion of each mandible; further flexibility of the mouth was provided by development of a transverse joint in the mandible between the anterior dentigerous and posterior articular segments. Large pointed teeth suitable for holding prey may well have already been present in the terrestrial ancestor, as they are in its closest living relatives, the monitor lizards; these however were modified by development of an expanded bony base in response to as yet unknown factors of the new environment.

Also in the Cretaceous a predatory bird took to the sea, and in time developed equally distinctive aquatic modifications. For swimming its rear limbs and feet became developed into powerful paddles —not the only means of swimming possible for birds but the most likely one. With the perfection of this type of locomotion these birds became so well adapted to life on the open water that ability to fly no longer was vital and loss of the wings followed, probably through a mechanism analogous to that which has reduced the wings of flightless insular birds. With their restriction to an aquatic existence (or quite possibly even earlier) fish became their chief if not exclusive food. Jaws which could better handle this slippery prey and also encompass larger mouthfuls of it were at a premium, and chance mutation permitted the same course of evolution which was followed by the contemporary mosasaurs, namely, loss of the anterior symphysis of the jaws and development of a transverse hinge. But the bones on which the latter developed differed in their extent, and the form and axis of the articulation differed from that of the mosasaurs, although it served

the same function. The teeth which were present in the jaws of the ancestor of *Hesperornis* may have become more important in the bird's economy as they became dominantly piscivorous. For reasons, which again, are unknown, they also acquired the swollen bases characteristic of the teeth of some aquatic reptiles.

It is noteworthy that both birds and lizards are preadapted for evolution of this type of swallowing mechanism by their movable quadrates.

The transverse mandibular joint permits outward bowing of the jaws to a greater extent than is otherwise possible without dislocation. This device allows the swallowing of much larger prey than would otherwise be possible. Among some recent fish-eating sea birds, notably cormorants and shearwaters (*Puffinus*), the mandibles are flexible in the region of the splenio-angular suture. These birds force relatively large fish down their throats; mutational development of a real articulation at this point might well be of value to such birds.

The similarities of the lower jaws of *Hesperornis* and the mosasaurs are thus seen to be adaptations to swallowing large and slippery prey, specifically fish. The structures are typical of convergence in the differences in detail of the intramandibular joint and essentially lacertilian palate of mosasaurs as opposed to the avian palate and beak of *Hesperornis*.

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THE STATUS OF THE SNAKE GENERA *DIPSAS* AND *SIBON*, A PROBLEM FOR "QUANTUM EVOLUTION"

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Some of the facts presented in this paper have been known so long that they can almost be said to have been forgotten. They are enshrined (or perhaps mummified) in generic names such as *Cochliophagus* 1853 (snail-eater), *Leptognathus* 1853 (delicate jaw), *Stremmatognathus* 1853 (twisted jaw), *Asthenognathus* 1854 (jaw without strength). These facts, and the problem posed by them to students of evolution, are our present knowledge of the structure, behavior, and relative abundance of the arboreal, nocturnal, and malacophagous snakes of the American Tropics, and their evolutionary relationship to other snakes in the American Tropics. While many generic names have been proposed for these snakes, *Dipsas* 1763 is the oldest, and it will be used (without prejudice) for the lot in this discussion. There are some 45 species.

Some, but not all, of the structural facts were known to Boulenger, the most recent reviser of snakes on a global basis. In 1896 he used the family name Amblycephalidae for *Dipsas* and some similar east Asiatic snakes.

THE GENUS *Dipsas*

The pterygoid bone of *Dipsas* (as in snakes in general) is firmly linked with the maxilla of the same side by the ectopterygoid, and the two bones function as a unit. In *Dipsas* the pterygoids are short, and do not diverge posteriorly to meet the ventral tip of the quadrate and the back end of the mandible. Among snakes in general the pterygoids are long, and their posterior ends are bound in with the quadrate and the mandible so as to form a single joint composed of the three bones.

It could be inferred, and it has been observed, that the arrangement in Colubrid and Viperid snakes was one which made the upper and lower jaw of the right side a protrusible and retractible pincer, a single functional unit, independent of a similar functional unit on the left side. It could be inferred that the two units might be protruded and retracted together or alternately at will, and both inferred actions have been observed in Viperid snakes (together in striking, alternately in deglutition). Alternate action in deglutition by Colubrid snakes has frequently been observed, but action together of right and left units (which may well occur in the initial bite) needs better observation for confirmation.

From the loss of the pterygoid connection between the maxilla and the mandible, it could be inferred that the arrangement in *Dipsas* was one that made each maxilla and each mandible separate functional units, all four of which could be protruded and retracted together, or moved in various combinations, or each independently. There is no information about the action in a living *Dipsas*.

In *Dipsas* the integument of the throat is composed of scales which may show a very irregular arrangement, and never show the normal snake arrangement of two pair of elongate scales (the genials) enclosing between them a groove (the mental groove) which is lined with elastic skin in the midventral line of the throat. It could be inferred that the mental groove functions as an especially elastic area in (a) deglutition, and (b) alternate

forward and backward movements of the mandibles in the same process. Very numerous observations confirm these inferences.

From the absence of a mental groove it could be inferred that deglutition in *Dipsas* snakes is a somewhat different process, in which there is no need for such an elastic midventral area, so that it has been obliterated by inelastic horny scales. As no one has reported seeing a *Dipsas* feed, this is merely inference of function from structure, as in paleontology.

It was noted as early as 1853 (*Stremmatognathus*) that some specimens had each lower jaw bent in a peculiar way, so that the anterior parts of them projected sideways out of the mouth and the long, needle-like teeth at the tips were exposed to right and left. Boulenger ignored this, as it seems to be a haphazard occurrence of death and fixation, and to have no systematic significance on the level of species or genera in the *Dipsas* group. On a family level, however, it might well have considerable significance, and on an evolutionary level it might represent a new adaptation. I have observed the phenomenon of the bent lower jaw in preserved individuals of several species. It appears to me that there is a functional hinge between the anterior (dentary-splenial) part of the lower jaw and the posterior (compound bone) part. It is unfortunate that no one has seen this hinge in operation. If the tip of each mandible could operate independently of the hind half there might be some functional correlation with loss of the mental groove, and loss of the pterygoid-mandible connection.

In 1931 Haas described and figured the head musculature of *Dipsas catesbyi*. He found a very unusual insertion of a part of the *adductor mandibulae* musculature, which I have verified on other species. In the typical snake the *adductor mandibulae* inserts on the hind portion of the mandible, and the insertion does not involve the dentary bone. In *Dipsas* a slip of this musculature inserts near the tip of the dentary. Haas calls this slip the *adductor externus superficialis 1a* (in the terminology of Edgeworth (1935) a part of the *adductor mandibulae externus anterior*). Haas apparently did not observe a specimen with bent jaw, and did not conceive of a joint in the middle of each lower jaw. He speaks of this muscle in functional terms as a *"sphincter oris."* I have observed the bent jaw situation in a number of specimens of *Dipsas,* and have seen the muscle in question taut, like a bowstring on a bent bow, and would suggest as a functional term for this muscle *"abductor dentalis."*

The facts and inferences presented so far indicate a marked evolutionary modification, a series of changes in the structures concerned with intake of food. The stomach contents have been stated to be slugs or snails (*Cochliophagus*). It is to be hoped that some day the feeding process will be observed (do the long teeth on the mandibles hook the snail out of its shell?). Most of the species seem to be rare, as will be shown for the countries I have studied, and they are very delicate, as are all these elongate, arboreal, nocturnal snakes. Such snakes wander abroad only during the period of highest relative humidity, and spend the day hidden in the damp interstices of bromeliads and tree holes, in immediate proximity to water if not actually in it. They die very rapidly from desiccation, as I have found to my sorrow.

The Genus *Sibon*

The anatomical modifications of these snakes have been considered of family or of subfamily significance by most students, but the existence of a single species has provided embarrassment to all. This is the wide-ranging and fairly common arboreal, nocturnal and malacophagous snake of the American Tropics *Sibon nebulatus* (*Petalognathus nebulatus, Sibon sibon*). Boulenger, who gave family

rank, straddled nicely by calling some specimens of this snake *Petalognathus nebulatus,* and others *Leptognathus leucomelas* (1894, p. 293; 1896, p. 453). A generic name for *Dipsas, Sibynomorphus* (shaped like *Sibon*), reflects this embarrassment, and Amaral, who gave subfamily rank, identified some Colombian specimens of this species as *Sibynomorphus mikanii oreas.*

In 1949 I went in the opposite direction and called this species *Dipsas nebulatus.* Thus a single species has been put into the family Colubridae and also into the family Amblycephalidae by so high an authority as Boulenger, and lesser lights have apparently been somewhat confused.

Haas (1931) described and figured the head musculature of *Sibon nebulatus,* and I have had ample opportunity to check his observations. The species is still embarrassing, and I have recently reinvestigated it.

It has (1) a mental groove flanked on each side by anterior and posterior geneials. It and they are not too well developed but are definitely present.

It has (2) normal Colubrid contact and joint of pterygoid with quadrate and mandible.

It has (3) very definitely *no* joint in the middle of the mandible.

It has (4) a forward extension of the *adductor mandibulae* musculature, perhaps similar in principle but different in detail (Haas speaks of it as intermediate), by no means so marked and definite as that in *Dipsas.*

It has (5) the dentition, the hemipenis, the body scalation, and the external form and appearance of *Dipsas.*

If a family or a subfamily division is made between *"Dipsas"* and "other snakes" *Sibon* belongs with "other snakes," but it is a close relative of *Dipsas* and occupies the "evolutional valley" between the "peaks" of ordinary snake adaptation and *Dipsas* adaptation.

Individual Abundance and Quantum Evolution

Simpson (1944) suggests that these "evolutionary valleys" may have been sparsely populated and passed through rapidly by means of "quantum evolution." It may be appropriate to enquire into the relative individual abundance and ranges of *Sibon* and of some of the species of *Dipsas.* Such an investigation discloses the following facts.

Sibon nebulatus has a range from southern Mexico to Ecuador and Brazil. This is a range far greater than that of any North American species of *Dipsas,* and greater than that of most if not all South American species. The range is comparable to that of all the species of *Dipsas* put together, although some species of *Dipsas* occur beyond the range of *Sibon nebulatus:* the west coast of Mexico to the north; in Paraguay, Argentina and Bolivia to the south; and apparently at some higher altitudes in the general range.

Collections of *Dipsas* vs *Sibon* cannot well be discriminatory as they have the same outward appearance, the same habits, and the same habitats. The relative number of them in collections is thus a random sample as far as they are concerned. In southern Central America the single species *Sibon nebulatus* occurs with eight species of *Dipsas.* I have examined all available material from Nicaragua, Costa Rica, and Panamá, and have seen 99 specimens of *Sibon nebulatus* and 41 specimens of *Dipsas.* This total can be broken down into countries: Nicaragua, 13 *Sibon,* 5 of 3 species of *Dipsas;* Costa Rica, 21 *Sibon,* 12 of 5 species of *Dipsas;* Panamá, 65 *Sibon,* 24 of seven species of *Dipsas.* A further breakdown for four contiguous lowland areas in Panamá can be found for *Sibon* (there called *Dipsas nebulatus*) and for two species of *Dipsas* in my account of the Panamá Snake Census for those areas (Dunn, 1949). In the lower Chagres basin in Panamá three of these snakes occur below the 500 foot line:

Dipsas nicholsi is endemic, unknown elsewhere, and only five specimens have been taken; *Dipsas viguieri* has been taken three times in the lower Chagres basin and also occurs in the lowlands and uplands of Darien; there are 12 specimens of *Sibon* from the area.

So far as reliable information goes, the intermediate, the species in the "valley," outranges and outnumbers the many species on the "peak," and the suggested rarity of anatomic intermediates is not supported by the facts. There seems thus some discrepancy between this case and the observed rarity of fossil specimens intermediate between families and between higher categories, and it is for this reason that I have presented it for consideration by other students.

(NOTE: Since the above was written, I have examined three more *Sibon* from Panama and one more *Dipsas*. Two unexamined specimens of *Dipsas* have been reported to me from Costa Rica and one of *Sibon* from Panama.)

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* It is somewhat ironical to find the best treatment of these snakes, considered as living organisms, in this paper of nearly 100 years ago.

ON ECOTYPIC AND AUTOTYPIC CHARACTERS, A CONTRIBUTION TO THE KNOWLEDGE OF THE EVOLUTION OF THE GENUS *LIOLAEMUS* (IGUANIDAE)

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INTRODUCTION

Few lizard genera are spread over so wide a region or have colonized such an extreme diversity of biotopes with their species and races as has the South American iguanid *Liolaemus*. The range of the genus is from the stormy coasts of Tierra del Fuego over nearly 40 degrees of latitude to the shores of Lakes Titicaca and Junin in Peru, and from the coasts of the Pacific across the Argentine pampas to the Atlantic. The species of *Liolaemus* are found in the evergreen forests of Chile, on the sand dunes and steppes of the lowlands in Chile and Patagonia, and in the barely inhabitable zones of the high Andes, and the high stony desert of Atacama. The Chilean and Argentine forms are separated for great distances by the mighty chain of the Andes, in which the passes are often at altitudes above 4000 meters, and are in the main impassable to ground dwelling poikilotherms.

The study of the evolution of a genus such as *Liolaemus* and of the species composing it is an attractive undertaking, of significant interest equally to the systematist and to the geneticist. Associated with the great geographic range are the facts that a series of regions have become habitable to these lizards only in the most recent geologic time, because they were covered by snow or glaciers during the glacial period, as in the higher Andean valleys; that other areas have developed their extreme environments only recently, as in the Atacama Desert; and finally that still other areas are subject to great and sudden environmental changes, as on the slopes of the active volcanoes. The great variety of biotopes is accompanied by a surprisingly high degree of variability within the genus. This makes the distinction of the species and their systematic arrangement extraordinarily difficult, but it is evidently this variability that has facilitated the colonization of such varied environments.

It is for the study of variable and polytypic genera that large series of specimens are most essential, and in regions with a great variety and sharp contrast of abiotic and biotic factors personal acquaintance with the biotopes is equally essential. These two requisites were fulfilled for me by the circumstance that a large amount of material had been accumulated in the Zoologische Staatssammlung, München, through the active efforts of Dr. Lorenz Müller, and by my own opportunities to acquire personal knowledge of the geoggraphy of Chile during my stay at the University of Chile. While in Chile, Dr. Wilhelm Goetsch and I were able to collect intensively, and friends increased our collections further. During a stay at the Naturhistoriska Riksmuseum in Stockholm I was able to examine the collections, mainly Patagonian, of *Liolaemus* there. Altogether some 3,000 specimens have passed through my hands (Hellmich, 1934, 1950a, 1950b).

The greater part of the material comes from Chile and from the Chilean-Argentinean frontier region in the high cordillera. The results here presented accordingly apply especially to Chile and to the Chilean species of *Liolaemus*. The study

[1] Translated from the German by Karl P. Schmidt.

of the non-Chilean material must await the examination of additional collections and perhaps further field study, and is reserved for the future.

Distribution of the Species and Subspecies of *Liolaemus* in Chile

If we attempt to form a picture of the distribution of the species and races of *Liolaemus* in Chile, a relatively simple presentation can be made by means of the two-fold tri-partite division of the country; into coastal cordillera, a longitudinal central valley, and high cordillera from west to east, and into desert, steppe, and forest from north to south. On the basis of present knowledge we can contrast a northern group of species, including *nigromaculatus* and *platei*, with the middle Chilean group *nitidus, chiliensis, lemniscatus, fuscus* and *gravenhorstii*, and with the south Chilean *cyanogaster, pictus*, and *tenuis*. To the east these are in contact with the forms of the high Andes, *lorenzmülleri, schröderi, monticola, nigroviridis, leopardinus, altissimus*, and *bürgeri*. At the extreme north in Tarapacá (according to information from M. Codoceo) the Peruvian and Bolivian forms *multiformis* and *alticolor* enter Chile; and in the extreme south a Patagonian form, *L. magellanicus*, also reaches the country (fig. 1). The systematic position of *Liolaemus* (*Helocephalus*) *nigriceps* of the desert of Atacama, of which I have only a single specimen available, is not yet clear.

As the northern and southern boundaries of the biogeographic regions interdigitate, so do the ranges of the species. Two such boundary lines appear to be more sharply defined and to have special faunal significance. The first is marked by the Cuesta de Chacabuco, whose effectiveness is strengthened by the Rio Aconcagua, and this forms the boundary between the subdivisions of the scrub-steppe region, the "Little North" and "Middle Chile"; at the same time it presents a barrier to the northward spread of southern forms. The second is the line from Co-

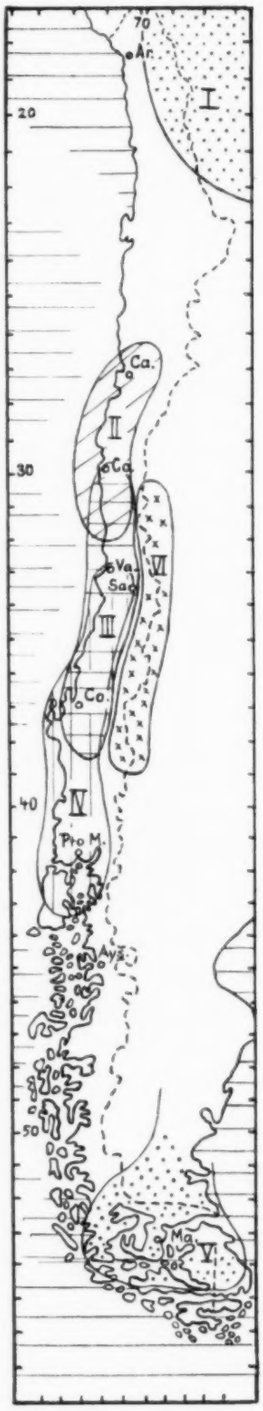

Fig. 1. Distribution of species of *Liolaemus* in Chile. Group I, *multiformis* and *alticolor;* II, *nigromaculatus* and *platei;* III, *nitidus, chiliensis, lemniscatus, fuscus*, and *gravenhorstii;* IV, *cyanogaster, pictus*, and *tenuis;* V, *magellanicus;* VI, *lorenzmülleri, schröderi, monticola, nigroviridis, leopardinus, altissimus*, and *buergeri*. The individual ranges overlap in part.

quimbo to La Serena and to Elqui, which forms the boundary between the "Little North" and the true desert region of North Chile. The boundary between the scrub-steppe and the forest, which extends east and west at about 27° South Latitude and is formed in the main by the Rio Bio Bio, seems to be less effective as a faunal barrier. The Cuesta de Chacabuco also forms a connection between the coast range and the high cordillera, over which *L. nigroviridis* has been able to pass from the Andes.

The ranges of the species in the plains are in general continuous, and the discontinuity of the two races of *L. platei* is therefore surprising. The typical form lives in the north, from Copiapó to Coquimbo; about six degrees of latitude farther to the south *Liolaemus platei curicensis* appears; the direct relation of the two forms is unquestionable.

The normal continuity of range on the plains contrasts with conspicuous discontinuity of the Andean forms. The only species with a relatively continuous distribution is *L. schröderi,* which ranges from Santiago to Villarica, at altitudes from 1500 to 2200 m, with what seems a surprisingly sparse population. The higher we go in the cordillera, the more marked are the discontinuities of distribution. At this level a number of species inhabit valleys that were beneath continuous snow and ice at the time of the glacial period. Their penetration of the new biotopes after the retreat of the glaciers does not seem to have been everywhere successful, for broad areas and many isolated volcanos were not reached, and have only a few of the usual latitudinally arranged series of species, or none. The Volcan Villarica is at the southern limit of the species that bear the stamp of the middle Chilean region. To what extent more southern forms of *Liolaemus,* ranging into the Andes from the east, have entered higher levels is as yet unknown. It is quite possible that the species *bürgeri,* occurring at the Planchon, is an immigrant from the eastern Argentine, since it has not been found elsewhere in Chile. It appears that the greater density of species on the eastern slope of the high Andes occurs farther south than on the western (Hellmich, 1950a). The greatest number of species, and thus presumably the optimum of environmental conditions, occurs on the western slope at the latitude of Santiago.

With the decreasing level of the peaks and the telescoping of the altitude zones, the areas inhabited by the species or races of the lizards are brought together so that on the Volcan Villarica there is an overlap of biotopes that may reach the extent of virtual coincidence, though ecologically the races can still readily be distinguished. At this point a series of forms enters Argentine territory via the low passes in the main range of the Andes. The interchange and interdigitation of the ranges of Chilean and Argentine forms has been discussed in greater detail elsewhere (Hellmich, 1950a).

The geographic races of the *nigromaculatus* group exhibit close areal relations, and are of especial biogeographic interest. In this group geographic forms may approach within a few meters, which would make for possible hybridization. It is not the races that are geographically most widely separated (with the range of the species as a whole) that are most differentiated, but those that live under the greatest extremes of ecological conditions. This fact may deserve to be generalized as an ecological rule.

The degrees of differentiation that appear in such series are to be set forth below. Unquestionably the investigation of these biotopes requires a much more thoroughgoing analysis than has hitherto been customary. As I have pointed out in my paper on the biogeography of Chile (1934), biogeographic investigation will doubtless require new methods. The data thus far given, usually for a single climatic factor, or even for temperature only, are not at all adequate. If one is to understand a living organism in its causal relations with its environment, consideration

of all of the factors will be necessary, in their daily, seasonal, and annual sequence. The development of an "aerobiology" of this sort is, in contrast with limnology, still at the most elementary stage. It appears to me that areas in which particular climatic factors reach extremes, as in deserts or under the severe conditions of high mountains, are especially suitable for such intensive study.

Variability within the Species of *Liolaemus*

The unusually great variability of the genus *Liolaemus,* one of the visible results of which is evident to the systematist in the continuing necessity for the description of new forms, extends to almost every characteristic. Variability in scale characters, in form and size, and in color and pattern may be matched in significance by variation in behavior. Before we had clarified the systematic relations we were often able to distinguish the individual species and races in the field by their behavior. Most of the species exhibit a considerable range of individual variation, within which certain characters have special taxonomic significance. Such significant characteristics are especially the size and form of the scales, the number of scales around the middle of the body, the development of the basic coloration and the arrangement of the elements of the color pattern.

Graphic representation of the variability of these characters usually presents normal curves of equal height and width. Within the range of a species lacking distinct races there may be geographic progressions that run parallel to climatic gradients, which may represent horizontal clines in the Huxleyan sense. This is most evidently true of the regularly increasing number of scales around midbody in species that range from warm dry areas to cool moist ones. The relative differentiation of body proportions were investigated in *Liolaemus* material by Miss Schuster (1950). The ground color corresponds to an astonishing degree with that of the general tone of the environment, with predominance of bright yellowish gray in desert areas, brown in the steppe, and dark green or blue in the forest.

Geographic variation, however, is especially characteristic of the species of *Liolaemus,* conspicuously in *L. nigromaculatus* of the northern deserts and steppes, in the Andean forms, and in forms whose range reaches the sea or extends to offshore islands.

In the species *nigromaculatus* the small races of the interior of the northern desert region (*atacamensis* and *copiapensis*) are connected with the large *ater* of the offshore islands by the intermediate *kuhlmanni* (farther south) and by *bisignatus* and *zapallarensis* on the coast. The coloration varies from that of *atacamensis,* with a pattern of bright-colored spots on a pale ground color evidently resembling the stony ground in the Atacama Desert, to the light greenish, almost patternless *bisignatus,* from the sand dunes at Caldera, and the strongly melanic *zapallarensis* of the coastal rocks at Zapallar and Papudo, and to the completely black *ater* of the islands. The race *bisignatus* exhibits an especially interesting morphological character in its shorter and more muscular tail, whose active lateral movements aid in digging into the dune sand. This reflex is exhibited also when the animal is placed on glass and stimulated.

The greatest amount of divergence, which may be parallel in different forms, is shown in Andean races of those species that have invaded the forest from the steppe; examples are afforded by *L. monticola* and *L. altissimus.* These divergencies may parallel the variation seen in species that do not exhibit subspecies though their range includes various biogeographic provinces. Comparison of the high Andes at Santiago with the mountains in the lake region (Villarica and Llanquihue) shows distinct climatic gradients that include several factors. The temperature becomes regularly lower, humidity increases, the summer season is shortened, the number

of days of bad weather increases, and insolation is reduced in intensity and in duration. The environmental conditions for poikilotherms range from an optimum at the north to a peius and finally a pessimum at the south. The following variation gradients in this direction can be observed:

1) Body size decreases.
2) Extremities become relatively shorter.[2]
3) The habitus as a whole becomes stouter.
4) Color and pattern darken in the sense of progressive melanism.
5) The size of the scales decreases, with increase in their number.

The behavior of the lizards also changes; the southern forms take a larger proportion of vegetable matter as food, and do not move so rapidly or for such great distances as do those from northern Andean regions. The flight reflex of the northern Andean forms is directed to distant rather than to nearby places of concealment.

Progressive variation in characters that parallels climatic gradients is also to be seen in the species whose range extends from the mainland to islands, as is the case with *pictus* and *nigromaculatus*. In this direction the changes are:

1) Increase of body size.
2) Darkening of color and pattern.

In the mountain and island melanism there are represented all three of the types defined by Reinig (1937) as "Melanism, s. str.," "Abundismus" and "Nigrismus." The lizards not only become darker in ground color, a process that may proceed from completely white to entirely black (Reinig's melanism proper), but also change the elements of the pattern, by broadening of dark markings (*nigrismus*), or by the appearance of additional ones (*abundismus*). All three types of melanism may be combined, or one or the other may predominate.

[2] The exceptions are listed by Schuster (1950).

Parallelism of characters unquestionably permits the conclusion that they have some close relation with the environment, for which reason I have referred to them elsewhere as "ecotypic." By this term I make no implication as to the usefulness or harmfulness of the character in question, or as to whether it is phenotypic or heritable, or, in the latter case, as to how it may have become heritable.[3]

Among the geographic races, however, we encounter changes in characters that in our view can have no definite relation with the environment. Such characters may consist of variation in the keeling of the temporals, of the throat scales, and of the dorsals; new arrangements of the head scales; and new kinds of sex-dimorphism. I should have liked to refer to such characters as "idiotypic"; but this term being in use for another concept, I suggest the term "autotypic," by which I wish to designate characteristics of geographic races that have no recognizable relation to the environment.

The objection can naturally be raised that the characters in question may in some way be linked with an ecotypic character. Like the atelic characters of Günther (1949), they may represent accessory effects of a pleiotropic gene. Such a gene may condition also a character with positive selection value, and the advantages offered by this character would have to outweigh the disadvantages or the mere burden of the atelic character. In this way an atelic character may indicate a physiologically conditioned but concealed selection value without being itself adaptive (Haldane, 1942, after Günther, 1949). This objection may be excluded at least in those cases in which subspecies of various species occur in the same or in closely associated biotopes and exhibit parallel ecotypic characters and divergent autotypic ones. If the latter were physiologically linked with the genes for the ecotypic characters they would also exhibit parallel development and could not vary from

[3] Compare the reference to Turesson's concept "ecotype" in Hellmich, 1934, p. 129.

this pattern. Examples of this kind of variation are afforded by various Andean species of *Liolaemus*. Thus the pepper-and-salt pattern seems to be an autotypic phenomenon in the males of *L. altissimus altissimus*, with no relation to the environment. This is true also of the different ranges of individual variation of the species *L. altissimus* and *L. monticolor* on the Volcan Villarica.

That the possibilities of autotypic characters are limited, and that we may not expect wholly new and novel characteristics is self-evident. The character designated as "ecological license' sets the framework within which they occur (Günther, 1949).

Ecological Significance of Characters within *Liolaemus*

In our attempts to find the correlations of the characteristics of a subspecies with its environment, the environment has thus far been thought of as a summarization of a variety of climatic and edaphic factors. The next question should be as to the possibility of seeking out the effective environmental factors for each case. We might do this by exclusion, by elimination, and by comparison of the differences in the biotopes that are being scrutinized. Such an attempt has often been made, and with the application of experiment, they have led to a great variety of results and of views. I call attention for example to the treatment of the literature by Reinig in the book cited. Very recently (1949) Eisentraut has summarized the views of various investigators as to which of the environmental factors are effective in conditioning melanism in island races of lizards. Eisentraut himself regards the altered nutritional conditions as the governing factor in the evolution of island melanism. Schuster (1950) regards both absolute size and relative size-relations of the appendages as correlated essentially with temperature. The same factor seems to govern in the differences in scale size and the correlated scale-number.

From my own observations and experiments I conclude that investigations thus far attempted are not at all adequate to make possible the correlation of a single climatic factor with the changes in question. I must repeat my belief that suitable methods of investigation are still to be sought, following the examples of limnology and microclimatology. I question further whether in any case a single factor is to be expected as *the* governing one. It seems certain that several factors combine to set the conditions under which a further summation of abiotic and biotic factors can become effective. It must be remembered that we are concerned with a living organism, in which stimuli from the external world again and again produce new and complex correlations.

This leads us inevitably to the question as to the ecological meaning of the variations that appear in the evolution of the varied races of *Liolaemus*. This has always been the viewpoint in the establishment of the "Geographic Rules." All of the clines of modification found among homoiotherms, such as the Bergmann and Allen Rules (cf. Rensch, 1947) seem to represent some ecological advantage in the sense of an adaptation, or at least to have selection value.

Whether a racial character is adaptive, atelic, or dystelic (cf. Günther, 1949) has nothing to do with the fact of its being ecotypic, at least within the framework of my definitions. Within the limits of the present discussion I cannot examine more closely these several kinds of concepts, which have by no means been uniformly employed. The concept "adaptive," as recently pointed out by Mayr (1947), has a double meaning, according as one sees in adaptation the results of a process or the process itself. If we hold to the definition of Mertens (1942), who quite excludes the idea of an adaptation in the Lamarckian sense from the idea of an adaptive character, applying this term only to mean that the character is useful in a particular environment or for a particular behavior, we unquestionably have an abundance of characters among the

Liolaemus races that are both ecotypic and adaptive.

In general this holds for the relation between bodily proportions and behavior, as in *Liolaemus nigromaculatus bisignatus*, and in the racial differences between *L. m. monticola* and *L. m. villaricensis* on the one hand and on the other *L. a. altissimus* and *L. a. araucaniensis*. It holds to a large degree for color and coloration. The melanotic coloration of island races of lizards has been interpreted as adaptive and as non-adaptive by various authors. Thus Mertens (1934) sees protective coloration only in the rarest cases in the melanism of island reptiles, since the most melanic lizards may have no enemies at all, and often live on quite light backgrounds; but he sees selective value in its great capacity for absorbing solar heat. Eisentraut (1949) rejects the idea of biological significance of island melanism for the Balearic Island lizards examined by him. The fact that the pigmentation of the protective pleura in *Lacerta sicula campestris* is involved in the blackening, leads Kramer (1949) to the assumption that island melanism has adaptive value. He thinks of it as the exclusion of harmful radiation, and of value for heat absorption, regarding the former as the more important. He regards a raised temperature-optimum of the organism as correlated with the greater capacity for absorbing heat.

As concerns island melanism, it would be extremely interesting to compare the pale desert *L. nigromaculatus atacamensis* with the melanic insular *zapallarensis* by means of refined examination of the environment, particularly with reference to radiation. It would also be interesting to test whether the black head and neck of *Liolaemus* (*Helocephalus*) *nigriceps*, of the high Atacama Desert, afford protection against the intensity of radiation at that altitude. The melanism of races in the high Andes of the south appears to me to be effective as a means of making use of the heat rays; for if it were as protection against too much insolation, the races to the north, at the latitude of Santiago, should be black, since there is both greater intensity and greater duration of radiation there.

If we analyse the adaptational value of the ecotypic characters of the South Andean races, it appears that the plumper form, the shorter appendages, the darkening of color and pattern, and the transition to a greater amount of vegetable matter in the diet may be adaptations to the cooler and moister climate, and that the smallness of the scales and their closer juxtaposition may reduce heat loss.

Such an adaptional value of many ecotypic characters contrasts with the fact that it is scarcely possible to discern an adaptive or selectional value for the autotypic characters. The non-adaptive nature of the autotypic characters is also indicated by the geographic distribution of the two types of characters. Geographic races of the Andean forms are not only to be found in widely separated areas, but are to be recognized also within more narrowly limited regions. Thus for example in the Santiago cordillera all the representatives of three species that occur in the valley of the Rio Volcan exhibit indications of geographic variation. This is in the vicinity of the mighty Volcan San José (5800 m). The climatic differences, if there are any at all, are naturally less marked than is the case with the ranges of species and subspecies that cover many degrees of latitude. It is noteworthy that these races, *Liolaemus leopardinus valdesianus*, *L. altissimus moradoensis*, and *L. nigroviridis minor*, are distinguished almost entirely by autotypic and not ecotypic characters. The tendency to reduction in size, especially notable in *L. n. minor*, could be interpreted as ecotypic, if one assumes other influences besides the climatic. A remarkable parallelism is to be observed in the gradation in size of the two populations of *Liolaemus buergeri*, which develops distinctively smaller forms in the vicinity of sulphur springs. It is conceivable that volcanic activity and attendant phenomena, such as poisonous

gases, might have an effect on growth. The stronger the climatic gradations the more sharply developed is ecotypic differenciation, and the greater is the number of such differences relative to the appearance of new autotypic characters.

A priori, the solution of the problem as to which ecotypic and autotypic characters are phenotypic or are genetically fixed does not belong to the field of systematics. Nevertheless, the current definition of "subspecies" and the coincident requirements of trinomial designation assume that subspecies are *not* to be based on nongenetic differences (Huxley, 1943). In practice, however, Dr. Lorenz Müller and I have built up our subspecific classification of *Liolaemus* on both types of characters (ecotypic and autotypic), and thus we regard them both as genetically anchored. I cannot discuss here the extensive literature that discusses this problem of genetic fixation of single racial characters. Breeding experiments, which afford the only unconditionally valid evidence, are difficult to carry out with reptiles. Those that have thus far been made in this group are not yet clearly interpretable. Melanic lizards of the genus *Lacerta* from the outer Faraglione islands, when crossed with mainland animals of the same species, produce intermediates that indicate mutations; on the other hand, the island form raised in captivity gradually becomes pale, which indicates direct environmental modification. The Chilean *Liolaemus* material would lend itself especially to such experiments and should yield valuable results in genetics and physiology.

Evolution and Disposal of the Species and Subspecies of *Liolaemus*

If we attempt to obtain a general review of the evolution of the various species and races of *Liolaemus* the most evident fact is that broad areas of the biotopes now inhabited have either changed greatly or have been invaded only very recently. A glacial age reigned in the southern hemisphere at the time of the northern Ice Age, and during this time the northern part of Chile was considerably more humid and the high Andes were covered throughout the year with continuous snow to a much lower level. The glaciers extended far out onto the plains and produced environmental relations that may perhaps be compared with the present day conditions on the west side of the Patagonian cordillera, with its great ice fields and glaciers extending to the sea.

A greater age must be assumed for the splitting up of the originally more compact genus *Liolaemus* into species, an age that extends backward into Tertiary times still little known. The geographic races, however, may unquestionably be regarded as post-glacial. The Andean ancestral forms moved successively into the areas freed from ice, a process in which there was a dispersal from north to south, perhaps at low altitudes, combined with a vertical expansion, and a north-south dispersal confined to higher levels. The latter process is indicated by the recently discovered *Liolaemus lorenzmülleri,* which is either the ancestral form, or one directly derived from it, from which the diverging *L. altissimus* and *L. leopardinus* have evolved; these two forms in turn have begun to give rise to additional races farther to the south. The distribution of *Liolaemus schröderi* in a north-south band also indicates such a mode of dispersal.

By this dispersal new biotopes were invaded, and these became more and more distinct with the progressive change of climate, and in connection with displacements of the vegetation cover, more and more isolated (fig. 2). Mutations spread through the originally small populations at a relatively rapid rate, and these favored the development of both autotypic and ecotypic characters; with the progressive divergence of biotic and abiotic factors selection pressure also increased. The major factor operative in the range of the *nigromaculatus* complex of subspecies was probably not expansion but the pro-

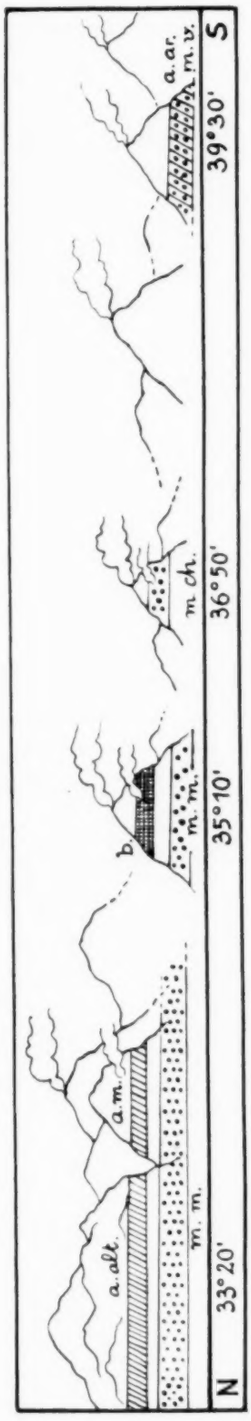

FIG. 2. Longitudinal profile through the high Andes from the latitude of Santiago to the Volcan Villarica (schematic and with the scale of height exaggerated). The ranges of the three species *Liolaemus altissimus, monticola,* and *buergeri.*

To the south the ranges of *monticola* and *altissimus* overlap; the latter species is absent on the Planchon and on Chillan. On the Planchon *L. buergeri* invades from the ? east. The altitudes of mountains and of the distribution zones become lower to the south. There is an accumulation of geographic races at volcanos and at fumaroles. Abbreviations: *a.a.—altissimus altissimus; a.m.—altissimus moradoensis; a.ar.—altissimus araucanicensis; m.m.—monticola monticola; m.ch.—monticola chillanensis; m.v.—monticola villaricensis; b.—buergeri.*

gressive change in the direction of aridity, bringing with it differentiation of the biotopes. Since the age of the climatic change is fairly well known, we have an approximate measure of the extraordinarily long time required for the evolution of these geographic races. According to Koeppen-Wegener (Hellmich, 1934) the last South American glacial advance is set at about 30,000 years ago.

Since the same ecotypic changes that serve for the differentiation of races operate to a lesser degree within a subspecies, the development of clines (in the sense of Huxley's horizontal clines) in a species of *Liolaemus* can be seen only as a gradual difference from the development of races. The geographic races we interpret as species *in statu nascendi.* For example, this is supported by the fact that a representation of the proportional relations within geographic races exhibits a scheme entirely similar to that found in various now distinct species.

It is naturally tempting to compare these views on the origin of the striking picture of variation presented by the genus *Liolaemus* in Chile with the newer ideas of evolutionary processes. Since there are various cases of emigrations from glacial refuge centers, the phenomena might be brought into relation with Reinig's *elimination* theory (1938). The expectation of Reinig that the range of variation becomes less toward the limits of the range is not at all the case in *Liolaemus.* The elimination of alleles postulated by Reinig contrasts with the appearance of the especially numerous ecotypic characters, the parallel nature of which permits the conclusion that they are intimately correlated with environmental relations and that they have high adaptive value. If we accept Dobzhansky's view that evolution in essence means disturbance of equilibrium, we may see in the fact of the development of so many subspecies and species the evolutionary process in an especially plastic genus that is meeting the requirements of new environments. This general process is reflected

also in the development of new characters by selection, within the framework of possibilities in the group, and in the attempt to establish the harmonious equilibrium, without which life on earth is impossible.

Among the releasing influences of the environment, the conspicuous fact that the vicinity of volcanos is especially rich in races might favor the conclusion that the special environmental influences in such areas might increase mutation-pressure.

Conclusions

The distinction between ecotypic and autotypic characters within the subspecies of the genus *Liolaemus* is intended to make a beginning toward our understanding of the relations of the characteristics of a highly variable genus with the strongly differentiating biotic and abiotic factors of the areas inhabited. The problem of the origin of these characters, and especially the problems of direct effects of the environment, or of directed sequence of mutations, or other theories, cannot be touched upon here. Chile cannot yet be regarded as fully explored as to its fauna. The wide areas previously uninhabited that have become open to colonization in postglacial times, and the great variety of environmental factors presented by these areas—which are unoccupied niches in the sense of Buxton—have afforded to the invading forms many possibilities for the development of new characters, in other words, have made possible the full expression of their intrinsic variability.

By the use of the concepts *ecotypic* and *autotypic* I have had no desire to increase the already vast terminology of the evolutionary vocabulary, but have hoped to clarify the confused variety of phenomena presented by the phenomena of variability. I hope to make a clearer systematic analysis by means of these concepts. More attention should be paid by specialists to the relations to the environment of the characteristics they employ in their description of new forms, and especially of geographic races. Such thoughtful descriptions would afford material for new investigation both in descriptive systematics and in systematics based on experiment. Experimental investigation of the kind of modifiability shown in *Liolaemus* should be especially fruitful. The readability of the too often entirely unrelated taxonomic works would be notably increased, and in addition such works would afford hints and clues to genetic research. Systematics, often despised, would thereby appear in a new light, and the call for cooperation between systematics and genetics, which seems to come much more from the geneticists than from the systematists, would then produce a fruitful response.

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CROSSING EXPERIMENTS WITH *CULEX* STRAINS

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INTRODUCTION

In medical entomology the Culicidae are in a dominant position because the carriers of the most frequent and feared tropical diseases (malaria, yellow fever, etc.) belong to this group. In accordance with this importance, ever since the discovery of the part they play as carriers, their systematics and biology have been to an increasing degree the object of scientific research, so that today one can say that they are the best known family within the order Diptera.

The systematics of this family has reached a certain peak and completion through the summarizing works of Martini (1931) and Edwards (1932). However, the complete speciation is not fully understood even up to this day. New species are still being described, especially from South America and the Pacific territory. The knowledge of the biology of the different species is still full of loopholes in spite of many known details. It has been best worked out for some of the *Anopheles* species. Here we feel the limiting influence of applied science which pays attention to the "important" species (the carriers) but frequently ignores the "unimportant" harmless species. In connection with the questions of distribution, breeding habits and susceptibility for certain parasites and the problems of combating them, the Culicidae have been used for physiological experiments, but our knowledge even in this field is very incomplete.

The systematics of the Culicidae is still entirely of the old school, using the morphology alone as the basis of its divisions. The Culicidae are a particularly clear example of how limiting this basis can be.

In general, the different representatives of a genus show only minor morphological differences. But the biological differences are considerably greater and well defined. Such biological differences led us to a realization that the holarctic "species" *Anopheles maculipennis* in Europe really consists of no less than five or six species (Bates, 1940). Up till now their differentiation could be made only on the basis of markings of the eggs. Lately, however, morphological differences for the adults have been found for the two palearctic species *Anopheles atroparvus* and *A. messeae* in the shape of the wing scales (Laven, 1950). Some further cases of so-called sibling species have become known in recent years; for instance *Anopheles gambiae* and *A. melas* in Africa. Many of the observations of differences of behavior in other species should be interpreted in part as meaning that the old, morphologically defined unit consists of two or more races, or in some cases even species.

Beside the already well worked out species complex of *Anopheles maculipennis* another group of holarctic Culicidae might be no less interesting, namely *Culex pipiens* and its nearest relatives. Up to now three species have been discerned in this group: *Culex pipiens* L., *C. fatigans* Wied. and *C. molestus* Forsk. The first species has its distribution in the temperate zone, the second one joins it in the south in subtropical-tropical territory. Within the distribution territory of *C. pipiens* was found in numerous places in Europe, North Africa and rarely also in North America a form which differed in its behavior from that of *C. pipiens*. While the latter is supposed to be exclusively a bird mosquito, feeding

[1] Translated by Mrs. Ernst Mayr.

predominantly or at least to a great extent on birds and domestic fowl, there was found in some places a very similar mosquito which molested man to a large degree. The feeder on man may possibly be *Culex molestus* which was described by von Forscai (1775) from Egypt. His description, however, contains only the vague demarcation that the insects were of a light color and did bite humans in Egypt. It will be the task of future investigations to determine which form should bear the name *Culex molestus* or if this name is at all tenable.

Two further pecularities can be attributed to the form which attacks man, by which perhaps it may be discerned from *C. pipiens*. First, its stenogamy, that is its ability to copulate in the smallest spaces, even a test tube, and second its autogeny, which is the ability to lay eggs without a previous blood meal. Whether these three traits, the attacking of humans, stenogamy and autogeny are really linked has still to be investigated. There are some indications that they do not always occur together. One knows of stenogamous *C. pipiens* strains (Callot and Dao Van Ty, 1943; Roubaud, 1933), which are not autogenous, one knows of *C. pipiens* attacking man, which are neither autogenous nor stenogamous. The separation of the different forms is therefore still quite uncertain and more or less arbitrary because reliable morphological characters are lacking.

Discussion of the Experiments

Among the forms which have the ability for autogenous egg laying are hidden several systematic units not yet recognized. This can be seen from crossing experiments which I made with such *Culex* strains. I succeeded in employing five of such strains, all autogenous and stenogamous, in the experiment. The first, called Hamburg in the following discussion, has existed since the middle of the 1930's in the Tropeninstitut in Hamburg and came from a population of mosquitoes which were molesting the people of Hamburg. The second strain, Immenrode (Harz), was raised in the winter of 1949/50 from hibernating mosquitoes. They were found in a small village near Goslar in the northern part of the Harz mountains. Mosquitoes of the same origin were taken out also of their wintering place in the winter of 1948/49. Their descendants, however, were crossed with the Hamburg strain and then raised purely autogenous. This strain which therefore originates from two populations will be called the "Hybrid strain" in the following discussion, without any intention of saying anything about its real genetic constitution. The third strain is of southern German origin, from Oggelshausen near the Federsee, and was started in the fall of 1950 from ten egg masses of wild mosquitoes. The descendants of all ten egg masses were in a high percentage autogenous and had to be combined for technical reasons into one strain, i.e. the strain Oggelshausen.

Besides these three pure strains and one hybrid strain from Germany I was able to include two additional strains from non-German territories for comparison: London and Paris. The strain London originated from mosquitoes which molested the people in the London subway during the last war (Shute, 1949). Strain Paris comes from mosquitoes from the environment of the French capital.

At this point I want to express my gratitude to Mr. P. F. Mattingly (Brit. Museum, Nat. Hist.) and Dr. P. G. Shute (Malaria Reference Laboratory, Epsom) to whom I owe the strain London, and to Prof. E. Roubaud and S. Ghelelovitch (Institut Pasteur, Paris) who have given me the strain Paris.

In addition to a thorough morphological comparison of these 6 strains, which is not yet completed, I have also conducted experiments in crossing them. For this purpose a number of virgin females (usually 5) were brought together with the

same number of males of a different strain. In this way, at least 25 to 30 matings in all of the combinations were completed. In case a female died before laying eggs, her seminal receptacles were examined to determine whether any sperm were present. All egg masses were observed for hatching or non-hatching. After all females of an experiment had laid eggs, they were killed immediately after the last laying and investigated for insemination.

Figure 1 shows the results so far obtained. Copulation was possible in every combination, and with a few exceptions all females were inseminated. With the eggs or died, it was impossible to deterof partner until the females had laid their females were kept together without choice technique used, whereby the males and mine whether sexual isolation between the strains existed. If it exists, it should probably be only a partial one, possibly somewhat graded. Egg masses were produced by all combinations, but only the

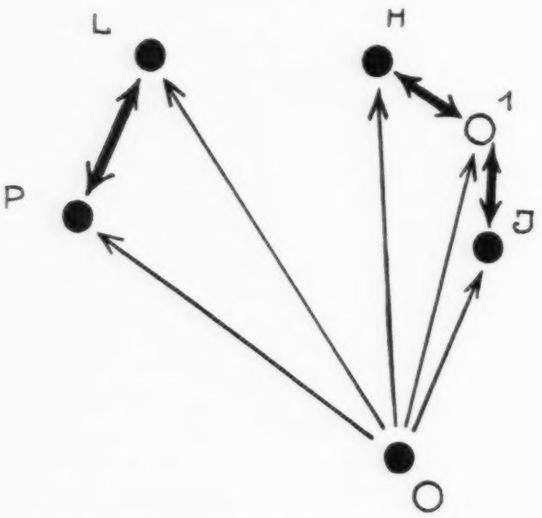

FIG. 1. Diagram of the crossing experiments of the author. The dots indicate the strain. H—Hamburg, 1—hybrid strain, I—Immenrode, O—Oggelshausen, L—London, P—Paris. The arrows are directed from the strain from which the males originated and point to the strains from which the females originated. Double-pointed arrows indicate crossing in both directions possible; single-pointed arrows indicate crossing only in one direction fertile.

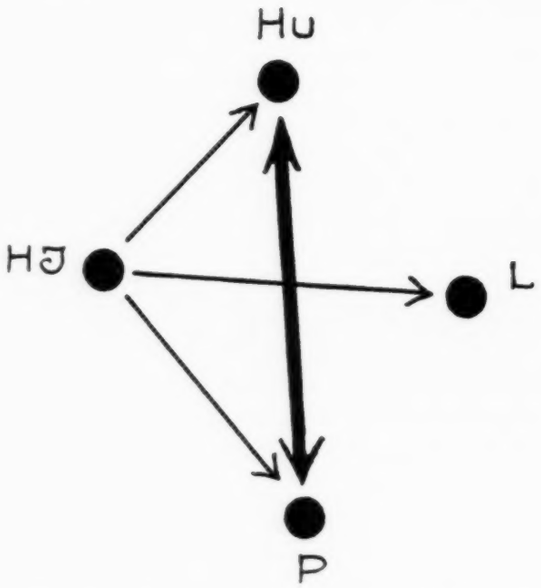

FIG. 2. Diagram of the crossing of Marshall (1938). HU—Hull, L—London (Westminster), HI—Hayling Island, P—Paris. For further explanations see figure 1.

eggs of certain of these crosses hatched. From a few of the egg masses which resulted from crosses that are really to be considered as sterile, a few larvae emerged which died immediately after the hatching or in the course of development in spite of the most careful rearing. Even the completely sterile egg masses generally contained embryos. Even those which did not show any development of an embryo were as a rule produced by inseminated females as was found later by dissection of the female.

The crosses between Hamburg (H), Hybrid strain (1) and Immenrode (I) were fertile in both directions. The same is true for Paris (P) and London (L). If we had known only this situation, we could have interpreted it, that we were confronted with two genetico-systematic units. But if we include the strain Oggleshausen (O) in the investigation, the interpretation of the results becomes more complicated. Males of this latter strain produce fertile descendants with females of all the other strains. The reciprocal crosses, however, resulted in eggs that were fertile but did not hatch.

In this way this strain proves to be an intermediate between all the other strains, but only in the male. Marshall (1939) has made similar experiments with the three English strains Hull (Hu), Westminster (L), Hayling Island (HI) and a French strain Paris (P) and reported briefly about this investigation (fig. 2). He succeeded in crossing Paris and Hull in both directions and his Hayling males produced descendants with the other strains, while all other crosses were sterile. Here too we have a strain whose males can fertilize the other females. It is too late to ascertain now whether this is identical with the German Ogglesshausen. We also have to consider that Marshall did not succeed in crossing Paris with London in any direction. However, I found fertility in both directions. From this we have to conclude that at least one of his strains, Paris or Westminster (London), was not identical with my strain from Paris and London respectively.

These findings among *Culex* strains which are similar in their autogeny and stenogamy according to the present investigations, but have a very different affinity among each other, become more complicated on account of the crossing experiments between *C. pipiens* and *C. molestus* on one hand and *C. pipiens* and *C. fatigans* on the other and also between *C. molestus* and *C. fatigans*. Several authors have made crossings of *C. pipiens* and *C. molestus*, usually with the aim to determine the genetics of autogeny (Roubaud, 1933; Vincent, 1933; Weyer, 1935; de Buck, 1935; Tate and Vincent, 1936; Roubaud, 1941). These were possible to a varied degree in both reciprocal directions with strains of very different geographical origins in Europe. At the present time it is not yet possible to bring system into these results because the experiments were made under very different conditions. The crossing *C. pipiens* and *C. fatigans* was undertaken by Farid (1949) in the United States. There resulted no differences in affinity between *C. pipiens* from Michigan and Baltimore and *C. fatigans* (*quinquefasciatus*) from Galveston (Texas) and a hybrid between these forms from the state of Mississippi or Alabama. Only rarely non-hatching egg masses were observed. On the other hand Weyer (1936) got copulation in crossings of *C. fatigans* and *C. pipiens* in both directions but no egg layings. Roubaud (1941) got 55 hybrids from crosses of *C. fatigans* females with *C. pipiens* males from about 300 eggs and with a crossing of *C. pipiens* females with *C. fatigans* males from about 850 eggs he got two hybrids. Weyer (1936) was able to cross *C. fatigans* and *C. molestus* in both directions and to raise the descendants up to F_2.

Conclusions

From all these experiments one thing seems evident: the systematic units of *C. pipiens, C. fatigans* and *C. molestus* so far recognized are not the last ones that need to be defined. Within these groups other units will have to be discerned, the rank of which (whether they are species, races or only genetically differentiated populations) cannot yet be determined with certainty. It is to be hoped that in the future further strains can be included in the investigation. It is especially important to clarify whether the units which are separated according to the present experiments are really allopatric.

In connection with crossing experiments of other Culicidae, interesting possibilities for genetic and evolutionary research can be opened up that deserve the greatest attention. The experiments within the *Anopheles maculipennis* complex cannot readily be compared with the aforementioned experiments with *Culex*. In the experiments with *Anopheles* species a disturbing fact is that only one, namely *Anopheles atroparvus*, is stenogamous and can be raised without interruptions. All other species are eury-

gamous and therefore it is impossible to make them reproduce themselves in the laboratory. Therefore one has mainly succeeded in crosses in which the males were *A. atroparvus*. It would diverge too much to include these experiments in our consideration. However, I would like to mention that here too crossings do occur, which are fertile in one direction and sterile in the other one (Bates, 1939). This is even more conspicuous in the crosses of *Aedes aegypti* and *Aedes albopictus* (Toumanoff, 1937, 1938, 1939, 1950; Downs and Baker, 1949) as well as in the crosses of *Aedes scutellaris scutellaris* with *Aedes scutellaris katherinensis* (Woodhill, 1949) which are fertile only in one direction.

About the genetics of single traits very little is known for the Culicidae. It is absolutely necessary to know more about this, in order to clarify further the described cases of different relationship between species, subspecies or strains of Culicidae, so that they can be compared with similar cases that are to be found in *Drosophila*. We could expect results of general interest from such investigations because of the different type of sex determination as shown in the Culicidae.

As for the rest, it has often been shown that a really exact clarification of the systematic position of the different carriers of disease has made possible the interpretation of peculiarities in the distribution of certain diseases, up till now incomprehensible. The exceptionally good information we have about the systematics of Culicidae, together with the knowledge about their distribution, is a challenge to further work in the direction of genetical research in this group.

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STRUCTURAL HETEROZYGOSITY IN NATURAL POPULATIONS OF THE GRASSHOPPER *TRIMEROTROPIS SPARSA* [1]

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Introduction

In former papers (White, 1949a and b, 1950, 1951) we have shown that the North American grasshopper genus *Trimerotropis* may be subdivided into two sections, a "primitive" one (A) in which all the chromosomes are acrocentric, and a "derived" one (B) in which some of the chromosomes have become metacentric, as a result of structural rearrangements which have transferred the centromeres from near the ends of the chromosomes to some interstitial position. Members of the related genera *Circotettix* and *Aerochoreutes* show the same type of genetic system as the members of section B of *Trimerotropis*. In order to simplify the terminology, we shall designate the assemblage of forms which possess some metacentric chromosomes as the "M.C." grasshoppers, a term which is not intended to correspond to any particular systematic category, but which probably represents a natural phylogenetic group. The M.C. grasshoppers consist, so far as known, of the section B of *Trimerotropis*, together with the genera *Circotettix*, *Aerochoreutes* and an unnamed genus which should be created to receive *Circotettix maculatus* Scudder, a species which is certainly not congeneric with *C. undulatus* Thomas, the genotype of *Circotettix*. If any of the Old World Bryodemae should eventually be shown to possess the same type of structural rearrangements in their chromosomes as the above-mentioned forms, they should be included in the M.C. group.

The chief cytogenetic and evolutionary interest of the M.C. group resides in the fact that in most of the species one or more chromosome pairs are represented by two acrocentrics in some individuals, by an acrocentric and a metacentric in others and by two metacentrics in yet others. A considerable proportion of individuals in the natural populations are hence structurally heterozygous and some populations consist almost entirely of structural heterozygotes. Just what type of chromosomal rearrangements have been responsible for the evolutionary conversion of acrocentric to metacentric elements is still uncertain, but it is clear from cytological observations of the meiotic divisions that crossing over in the structurally heterozygous bivalents does not lead (at any rate in the male) to the production of acentric and dicentric chromatids (except for one instance to be discussed later). In a population in which n chromosomes are heteromorphic there will be 3^n types of individuals (in *Trimerotropis thalassica* the work of King (1924) suggests that n is at least 9, indicating the existence of a minimum of 19,683 types of individuals).

Not all the species belonging to the M.C. group show structural heterozygosity, since in *T. pallidipennis* there seem to be invariably three pairs of metacentric autosomes and eight pairs of acrocentrics and preliminary studies indicate that an essentially similar situation exists in *T. diversellus*, *T. saxatilis* and *T. schaefferi* (except that in the two latter species there are four pairs of metacentrics and seven pairs of acrocentrics).

The present paper is a sequel to one recently published (White, 1951) in

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which we reported on the cytological conditions in four populations of *Trimerotropis sparsa,* three in western Colorado and one in northern New Mexico, the material having been collected in 1949. As a result of much more extensive collecting in the summer of 1950, we are now able to describe the cytological composition of many more populations in Colorado, Utah and Nevada. The total number of localities at which we have collected the species is now 29, and the number of male individuals which have been analyzed cytologically is 762.

Trimerotropis sparsa is a member of section B of the genus *Trimerotropis* which shows an extreme degree of structural heterozygosity. In addition, some individuals possess heterochromatic [2] supernumerary chromosomes in addition to the normal complement, and in certain areas of northwestern Colorado and northeastern Utah a chromosomal fusion between two autosomes is present, which, when homozygous, reduces the diploid number of the male from 23 to 21. The cytological picture is thus highly complex, each population having its own characteristic cytological facies.

Distribution and Ecology of *Trimerotropis sparsa*

The total geographic range of *T. sparsa,* as far as we have been able to determine it from our own collecting, literature records and specimens at the Academy of Natural Sciences, Philadelphia, is shown in figure 1. Within the area enclosed by the dashed line *T. sparsa* is absent from all the mountainous areas (above 7,000 ft.) and also from forested or cultivated regions at lower elevations. It is, in fact, almost completely restricted (at least in Colorado, Utah and Nevada) to the so-called shadscale zone (Billings, 1945, 1949), in which the dominant vegetation consists of several species of more or less spiny, microphyll, chenopodiaceous shrubs of which the principal one is *Atriplex confertifolia.*

Within the shadscale zone, *T. sparsa* is not ubiquitous, but occurs especially on dry mud-flats or playas and on eroded "badland" hillsides. The principal vegetation on the playas is nearly always *Sarcobatus vermiculatus* Nees. On the badlands and hillsides *Sarcobatus* may occur to some extent, but *Atriplex confertifolia* (or *A. cuneata* A. Nels. in western Colorado) is the dominant shrub. Grasses are largely absent from these playas and eroded slopes during the summer months and the ephemeral herbs which were present at the beginning of the summer are mostly dead by the end of July. We therefore conclude that *T. sparsa* must feed, at least in the imaginal state, on various Chenopodiaceae. An excellent ecological description of one typical *Sarcobatus* flat on which we collected *T. sparsa* (the one in White Valley, Millard Co., Utah) is given by Fautin (1946, p. 268).

Since *T. sparsa* is not normally an inhabitant of the "Transition zone" and is hardly ever found above 6500 feet, it is confined in western Colorado and eastern Utah to the river valleys. Along these valleys ecological conditions suitable for *T. sparsa* are fairly continuous, except where extensive cultivation is practiced. Thus it is probable that the collecting localities which we have called Cedar Creek, Olathe, Delta and Whitewater represent points at which we have sampled an essentially continuous "Gunnison Valley population." Similarly, we believe that the collecting localities De Beque, Rifle I and Rifle II are not separated by any territory unsuitable for *T. sparsa* and that these populations are probably continuous in the same way. On the other hand the valleys of the White and Yampa rivers are separated from the upper Colorado valley by the high Roan plateau, which is totally unsuited for *T. sparsa.*

[2] The supernumerary chromosomes are, in reality, only partially heterochromatic, since they contain euchromatic segments. The heterochromatic segments are, however, much more conspicuous and are probably more extensive.

We therefore believe that the Meeker and Piceance Creek populations are separated by a real geographical barrier from those at De Beque and in the vicinity of Rifle.

The situation in the Great Basin area is entirely different. Here *T. sparsa* occurs in the floors of a series of parallel north-south valleys separated by fault block mountain ranges. In general, each of these valleys is an enclosed basin and consequently each supports a population of *T. sparsa* which is geographically discontinuous from those in the adjoining valleys, being separated by sagebrush-covered (and in some instances pine-clad) mountain ranges. Such populations as those collected at White Valley, Robinson's Ranch, Cherry Creek and Railroad Lake are hence, in all probability, effectively isolated from one another at the present time. The populations collected in the Humboldt valley (Lovelock, Rye Patch Dam, Battle Mountain) are, on the other

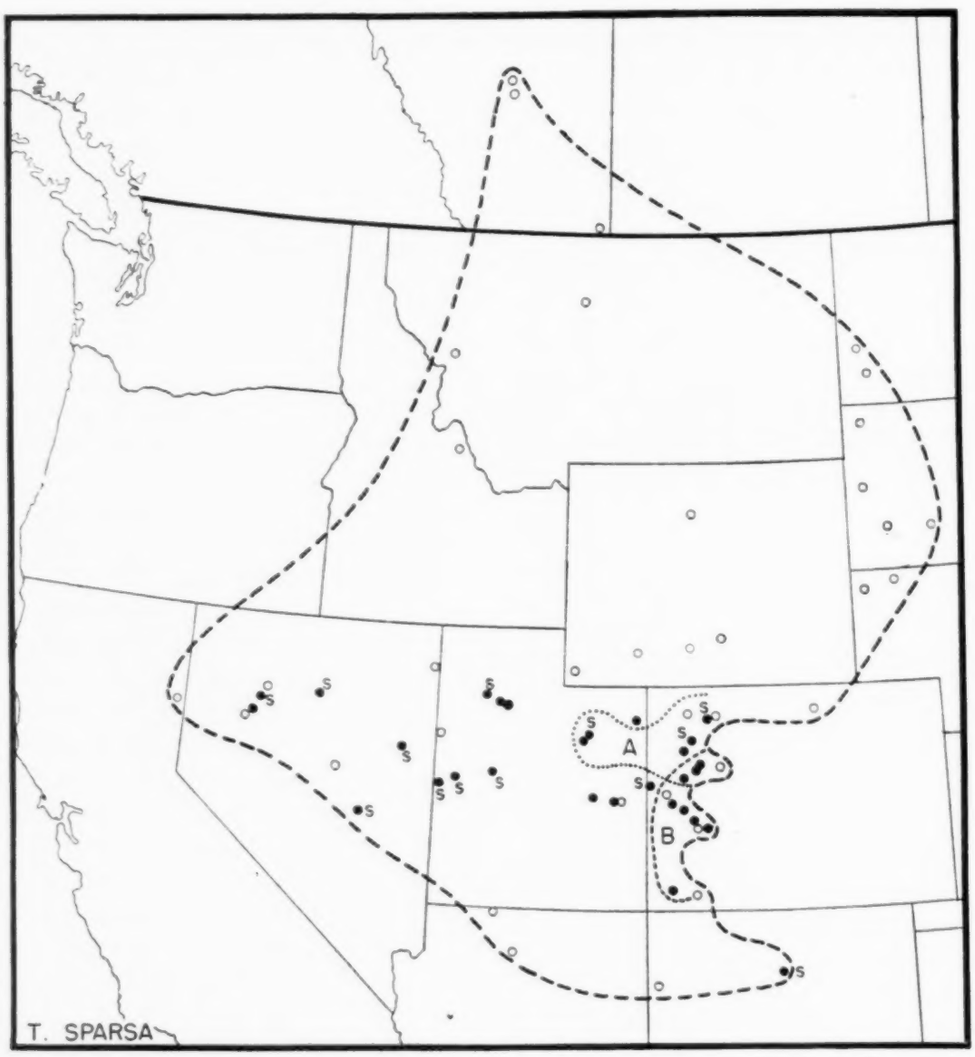

FIG. 1. Map showing (dashed outline) the approximate distribution *Trimerotropis sparsa* in western North Ameria. Black circles, localities where we have collected the species; hollow circles literature records or specimens in the collections of the Academy of Natural Sciences, Philadelphia. A is the area within which the chromosomal fusion has been found, B the area from which supernumerary chromosomes appear to be absent. The symbol S alongside a locality indicates that supernumerary chromosomes have been found in that population.

TABLE 1. *Origin of material collected in 1950*

Locality number		Date	Number of males	
			Collected	Analyzed cytologically
	Colorado			
1.	Cedar Creek, 6550 ft., Montrose Co.	VII.18	32	31
2.	4 mi. N. of Olathe, Montrose Co.	VII.18	16	16
3.	10 mi. W. of Delta, Delta Co.	VII.18	5	5
4.	2 mi. NE. of De Beque, 5150 ft., Mesa Co.	VII.20 & VIII.11	6	6
5.	Hillside above Government Creek, 7 mi. NNW. of Rifle, 5920 ft., Garfield Co., ("Rifle I")	VII.19	8	8
6.	3 mi. W. of Rifle, 5400 ft., Garfield Co. ("Rifle II")	VII.20 & VIII.11	6	6
7.	Piceance Creek, 6000–6250 ft., Rio Blanco Co.	VII.19 & VIII.10	5	5
8.	7 mi. W. of Mack, Mesa Co.	VII.21 & VIII.12	55	54
9.	McElmo Creek, 4½ mi. E. of Cortez, Montezuma Co.	VIII.13	16	16
	Utah			
10.	Crescent Junction, 5070 ft., Grand Co.	VII.21 & VIII.12	4	2
11.	3 mi. W. of Greenriver, 4100 ft., Emery Co.	VII.21	3	1
12.	3 mi. N. of Jensen, near entrance to Dinosaur National Monument, Uintah Co.	VIII.9–10	37	35
13.	Indian Creek, 2 mi. SE. of Duchesne, Duchesne Co.	VIII.9	26	26
14.	Indian Creek, 11 mi. SE. of Duchesne, Duchesne Co.	VIII.8	2	2
15.	15 mi. E. of Grantsville, Tooele Co.	VIII.7	1	—
16.	5 mi. NW. of Grantsville, Tooele Co.	VIII.7	1	—
17.	3 mi. W. of Delle, Tooele Co.	VIII.7	23	21
18.	3 mi. N. of Hinckley, Millard Co.	VII.23	25	23
19.	White Valley Sarcobatus Flat, Millard Co. (junction of Partoun Rd. and U. S. 6)	VII.24	11	11
20.	3 mi. E. of Robinson's Ranch, Millard Co.	VII.24	7	7
	Nevada			
21.	5 mi. SE. of Cherry Creek, White Pine Co.	VII.25	63	58
22.	Railroad Valley Sarcobatus Flat, Nye Co.	VII.26	22	22
23.	5 mi. NE. of Lovelock, Pershing Co.	VIII.2–3	5	5
24.	Rye Patch Dam, Pershing Co.	VIII.5	15	14
25.	Battle Mountain, Lander Co.	VIII.6	30	29
			424	403

hand, probably parts of a continuous "Humboldt Valley Population."

The exact localities at which the material was collected in 1950 are listed in Table 1. No attempt was made to ascertain the actual population-size or density at any of these localities, but the species was extremely abundant at locality 8, relatively common at localities 1, 2, 3, 9, 12, 13, 17, 18, 19, 20, 21, 22, 24 and 25, and rare at localities 4, 5, 6, 7, 10, 11, 14, 15, 16 and 23.

CYTOLOGICAL OBSERVATIONS

In describing the cytological conditions in the various populations we are concerned with three types of variability, (1) supernumerary chromosomes, (2) the chromosomal fusion already mentioned, (3) the special type of structural heterozygosity which is characteristic of the majority of the M.C. species. We shall first of all consider each of these separately and then describe the cytological

composition of the different populations.

Supernumerary chromosomes were present at three out of the four populations sampled in 1949 (details in White, 1951), but were absent from the sample collected at Whitewater, Colorado. We can now state that the other populations in the Gunnison valley (Cedar Creek, Olathe and Delta) resemble the Whitewater population in lacking supernumeraries, and the same was true of the small samples collected at De Beque, Rifle I and Rifle II (for the location of these collecting-stations see Figs. 2A and 2B). The Cortez and Jensen populations also appeared to lack supernumeraries, but in the Mack population one individual (out of a total of 54) possessed a supernumerary. There is hence an area of western Colorado (which probably extends into eastern Utah) in which supernumerary chromosomes are absent from the genetic structure of the species, or at any rate present in a much lower frequency than elsewhere. This area is indicated in figure 1 ("B"). Supernumerary chromosomes were found to be relatively common in material from Craig and Meeker, Colorado and Pojoaque, New Mexico (White, 1951), and they have since been found to occur also in the Great Basin populations (table 5).

In most populations where supernumeraries are present, there are two types of them, one acrocentric and the other metacentric. We have already suggested,

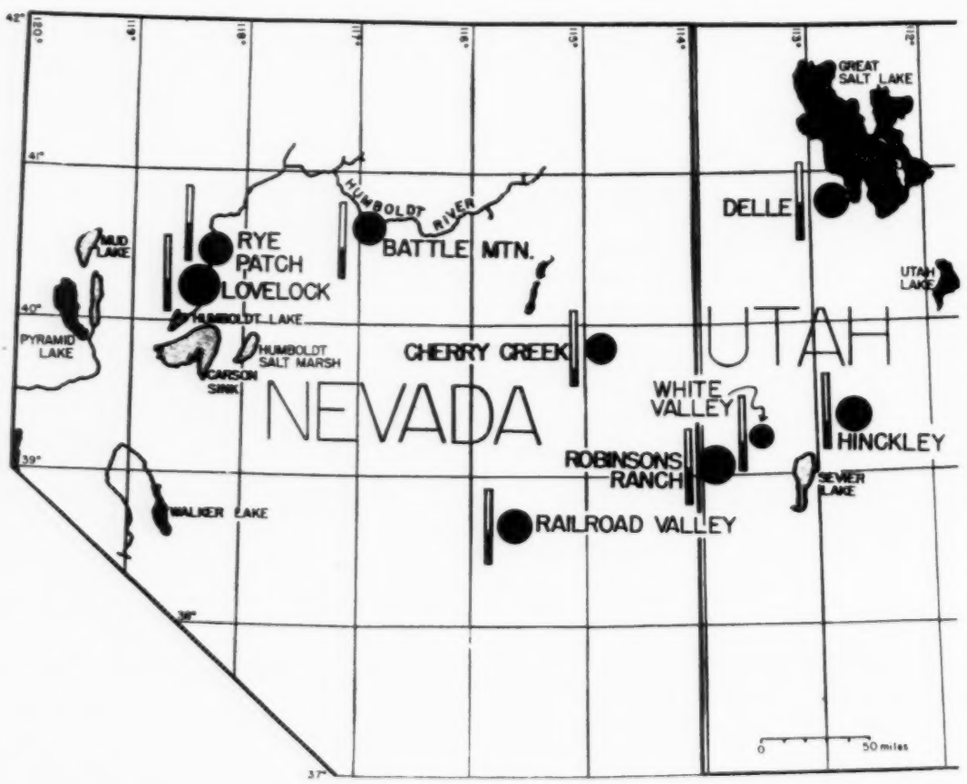

FIG. 2A. Map of northern Nevada and western Utah, showing the cytological characteristics of the Great Basin populations of *Trimerotropis sparsa*. The size of the black circles represents the degree of heterozygosity of the populations (i.e. the mean number of heterozygous bivalents per individual). In the case of Cherry Creek the size of the black circle represents the heterozygosity of the males only (in this population the females show a higher degree of heterozygosity than the males, due to the existence of two structurally different types of X's). The black parts of the histograms alongside each locality represent the mean number of metacentric chromosomes, the white portions the mean number of acrocentric chromosomes.

FIG. 2B. Map of eastern Utah, western Colorado and northern New Mexico, showing the cytological characteristics of the "eastern" populations of *Trimerotropis sparsa* (this map is a continuation of figure 2A, on the same scale). Symbols as in figure 2A. The symbol for the Rifle II population is shown cross-hatched, for convenience, since it overlaps that for Rifle I.

on the basis of their meiotic behavior, that the latter are probably isochromosomes. At localities 8, 13, 19, 20 and 25 only the acrocentric type of supernumerary was encountered, but it is probable that if larger samples from these localities had been available for study metacentric supernumeraries would have been found in some of them. At localities 17 and 18 metacentric supernumeraries were found, but no acrocentrics; again it is possible that if the samples had been larger both types of supernumerary would have been encountered.

We have already described (White, 1951) the meiotic behavior of the supernumerary chromosomes, and only a few details will now be added. These are based mainly on a study of one of the individuals from Cherry Creek, which possessed two acrocentric supernumeraries and an isochromosome supernumerary. The arms of the latter are exactly equal in length and each arm can be seen, during diplotene, to consist of a large proximal heterochromatic segment, followed by an interstitial euchromatic region and a minute distal heterochromatic blob. Chiasma-formation was studied in a large number of diplotene nuclei in this individual. At this stage the supernumerary chromosomes could be very clearly recognized by their characteristic degree of heteropycnosis (fig. 5a); the X is also heteropycnotic, but there is no possibility of confusing it with the supernumeraries. In all the diplotene nuclei studied the two acrocentric supernumeraries were invariably paired with one another and showed no tendency to pair with either the X or the isochromosome supernumerary. They seem to be invariably connected by a single chiasma which may be either interstitial or nearly terminal (fig. 5b).

The appearance of the isochromosome supernumerary in these diplotene nuclei is highly characteristic. It forms a small ring, about two-thirds of whose circumference is heterochromatic, the remaining third being euchromatic. A single chiasma between the two arms of the isochromosome is regularly present in the euchromatic part of the ring, i.e. in the distal segments of the two arms (fig. 5a, c). The presence of this chiasma no doubt accounts for the doughnut-shape of the chromosome at first metaphase (fig. 5d).

The fact that no pairing ever takes place between the metacentric and the acrocentric supernumeraries probably indicates that there is little or no homology between them. On the other hand, it is possible that the two arms of the isochromosome, being very close together, always pair before there has been a chance of either of them pairing with the acrocentric supernumeraries.

At first metaphase (fig. 5d) the isochromosome supernumerary regularly lies off the equatorial plate, usually near one of the poles of the spindle. The bivalent formed from the two acrocentric supernumeraries, on the other hand, is orientated in the equatorial region of the spindle like any ordinary autosomal bivalent, and could only be identified at this stage because it is somewhat thicker than any

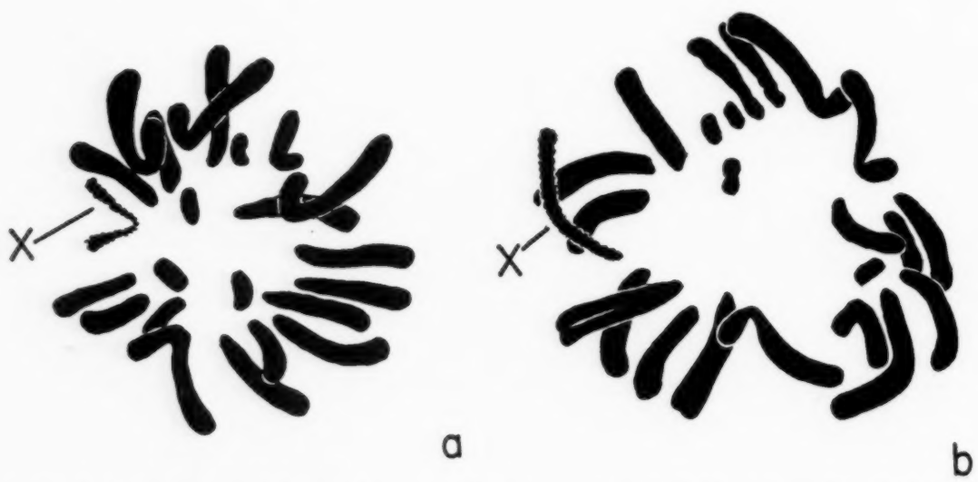

FIG. 3. Spermatogonial metaphases of *T. sparsa*. a, an individual from Lovelock with a metacentric X and six metacentric autosomes; b, an individual from Cherry Creek with an acrocentric X and five metacentric autosomes. In both cases one of the metacentric autosomes is no. 10.

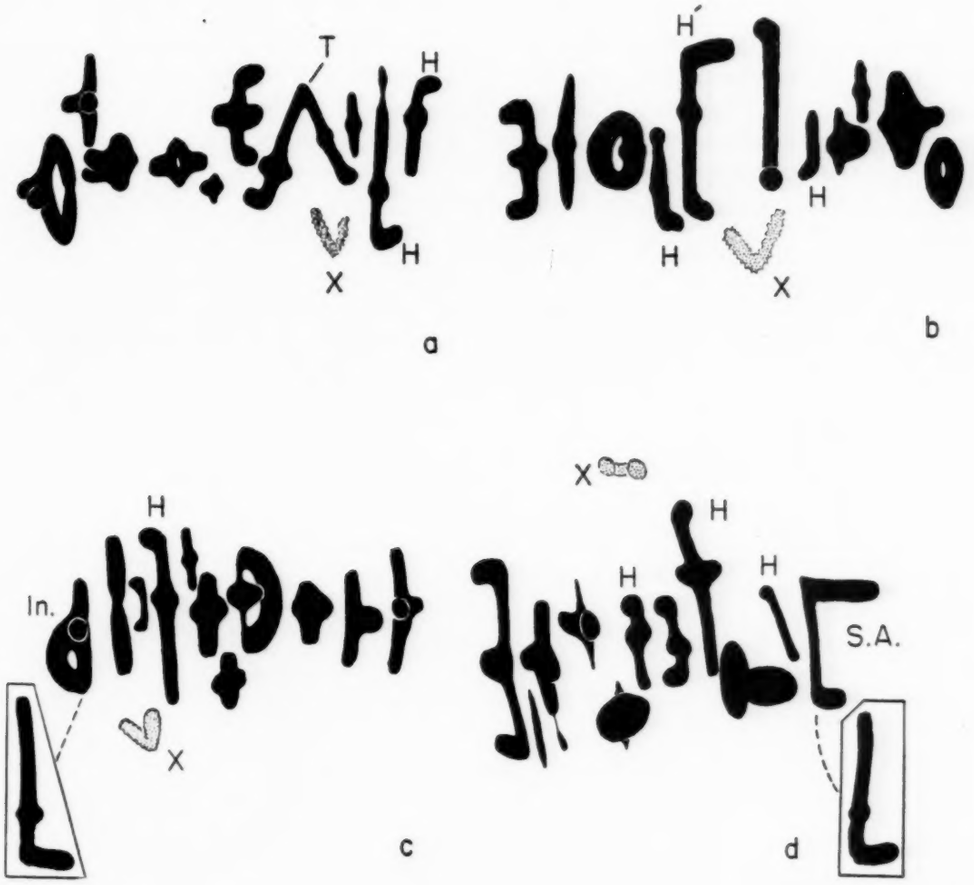

FIG. 4. First metaphases of *T. sparsa*, showing various unusual conditions. a, the individual from Duchesne which was heterozygous for the chromosomal fusion and shows a characteristic trivalent (T); b, an individual from Olathe in which there is a structurally heterozygous bivalent (H′) composed of two metacentrics; c, a cell from one of the Cherry Creek individuals with a bivalent which shows a chiasma in the "internal segment" as well as in the "external segment" (the insert shows the usual appearance of this bivalent in other cells of the same individual); d, a cell from an individual collected at Battle Mountain with a bivalent (S.A.) which has a chiasma in the short arm (the insert shows the usual appearance of this bivalent). In all figures structurally heterozygous bivalents with a chiasma in the external segment only are labelled H.

of the autosomal bivalents. In an individual from Craig, Colorado, described in our former paper, a bivalent composed of two acrocentric supernumeraries rather frequently orientated itself in such a way that both centromeres were directed toward the same pole, the bivalent having a U-shape (White, 1951, fig. 2), but this type of behavior was not seen in the Cherry Creek individual.

The chromosomal fusion which we have already mentioned has only been found in area "A" shown in figure 1, but the northern boundary of this area is quite uncertain and it may extend into Wyoming, Montana and the Dakotas, from which we have no material.

All the 27 populations of *T. sparsa* which we have analyzed cytologically show some degree of structural heterozygosity in respect of centromere transpositions. This is, in itself, a strong *a priori* argument in favor of the view that the structural rearrangements have some adaptive significance, since otherwise one would expect that some, at least, of the populations would have become structurally monomorphic as a result of

"drift." The same situation seems to occur in *T. gracilis, T. cyaneipennis, T. pseudofasciata, T. suffusa, Circotettix undulatus, C. rabula, C. coconino, C. crotalum* and *"Circotettix" maculatus,* in all of which species we have never found a population without chromosomal polymorphism.

In spite of this strong circumstantial evidence that the structural rearrangements present in all populations of these species are adaptive, no definite proof for an adaptive role has yet been obtained. *T. sparsa* seems to be a rather unsuitable species in which to carry the analysis further, since the number of different re-

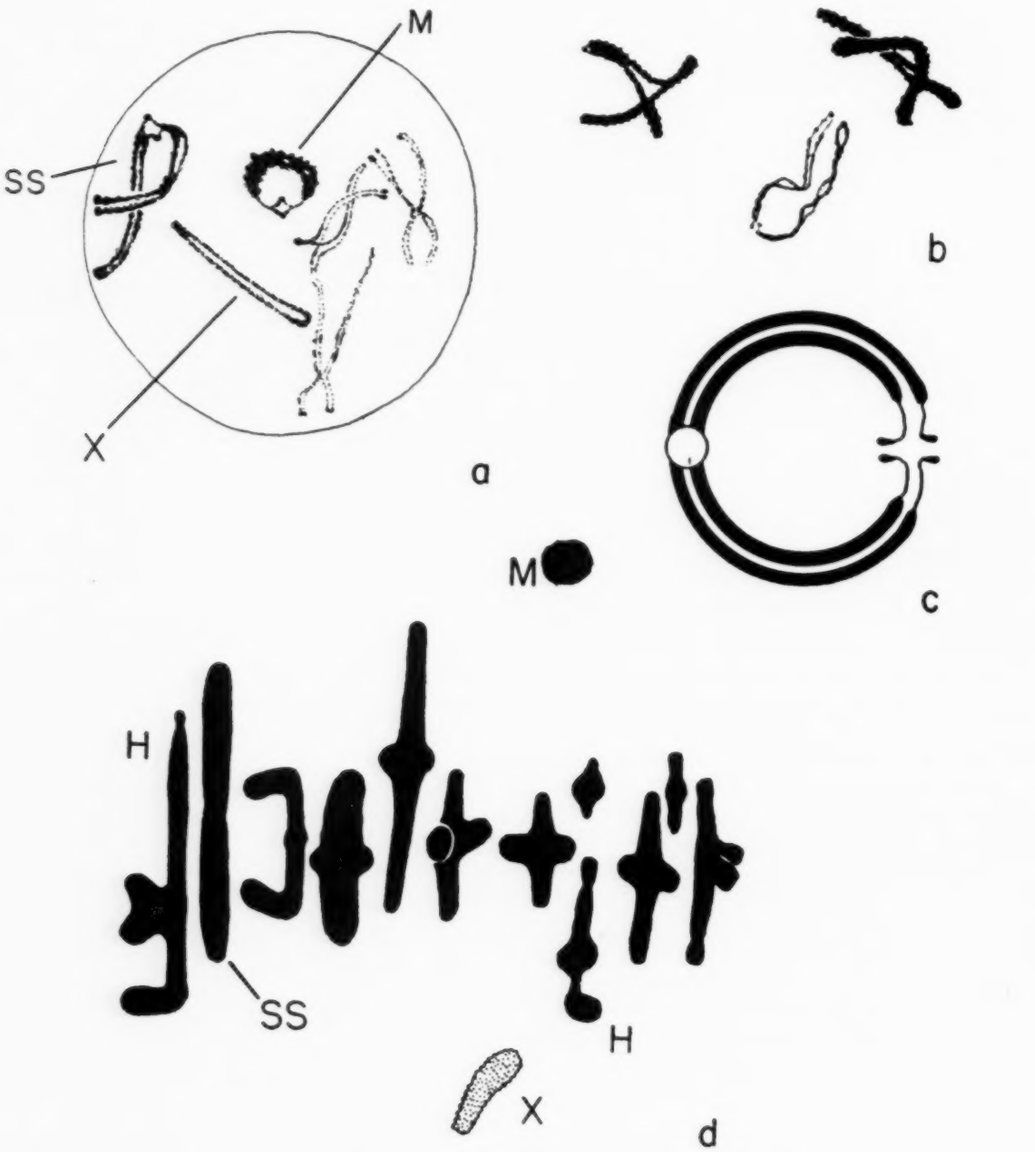

FIG. 5. Meiosis in an individual from Cherry Creek with an acrocentric X-chromosome, two acrocentric supernumeraries and an isochromosome supernumerary. a, diplotene, showing the X, the bivalent formed by the two acrocentric supernumeraries (SS), the isochromosome (M) and three autosomal bivalents (the other eight are not shown); b, the appearance of the SS bivalent in three different diplotene nuclei, showing the variable position of the chiasma; c, a diagram of the isochromosome supernumerary, with a chiasma between its two arms; d, a first metaphase, showing the SS bivalent stretched on the spindle and the doughnut-shaped isochromosome (M) near the upper pole.

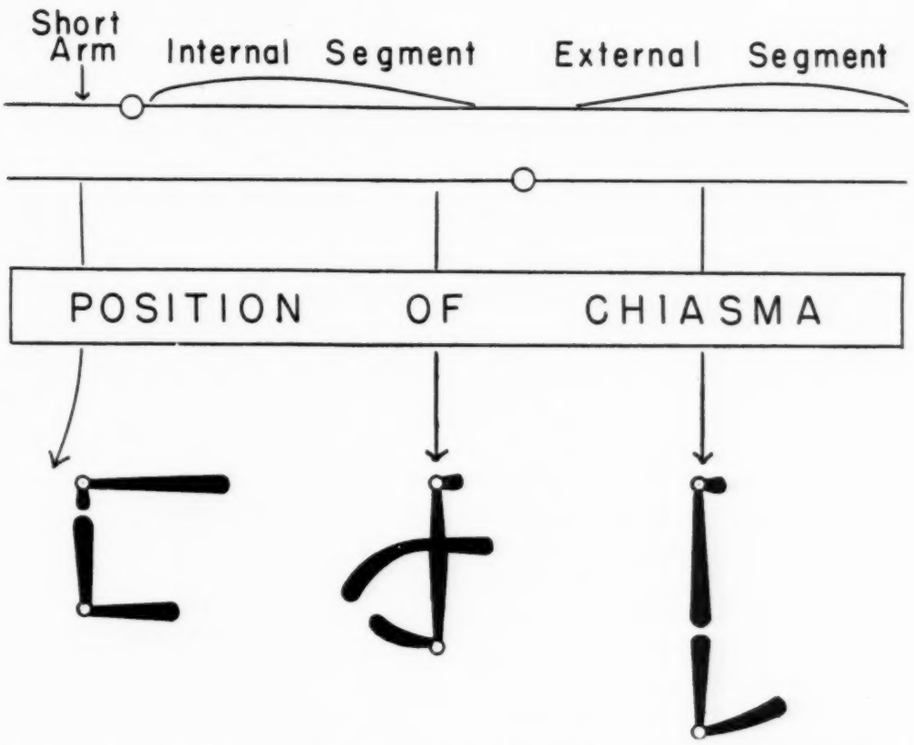

FIG. 6. Diagram to show how the position of the chiasma in the structural heterozygous bivalents of *T. sparsa* determines the appearance of the bivalent at first metaphase. Ordinarily, chiasmata are confined to the external segment.

arrangements is relatively large and they cannot in most cases be individually identified with certainty.

We have endeavored to obtain some idea of the total number of different structural rearrangements which are present in *Trimerotropis sparsa,* but such calculations can, of necessity, only lead to a minimum estimate, since in most cases we have no means of determining whether two rearrangements in different populations which appear to be the same are in fact identical.

Of the 11 pairs of autosomes which are usually present (i.e. neglecting for the present the chromosomal fusion which is present in area "A" of figure 1), one pair (probably the largest) seems to invariably consist of two metacentric chromosomes, in all the populations studied. The smallest chromosome pair, on the other hand, always seems to consist of two acrocentric elements. The remaining nine autosomes are "heteromorphic," i.e. they may be either acrocentric or metacentric, and in at least two of them there are two different metacentric types as well as an acrocentric type. Thus, if we take an individual of the constitution X_m MAAAAAAAAAA as the "standard" (where X_m represents a metacentric X, M a pair of metacentric autosomes and each A a pair of acrocentric autosomes), then at least 12 structural rearrangements are present in the species, each "rearrangement" being defined as a chromosome type which can exist in the heterozygous condition with a "standard" chromosome. Actually, no individual with the "standard" chromosome set formulated above has actually been found, but at Cherry Creek we collected several of the type X_m MHAAAAAAAAA (where H represents a structurally heterozygous bivalent composed of an acrocentric and a metacentric chromosome), so that there can be little doubt that if the sample had been larger one or more individuals with the "standard" formula would have been encountered.

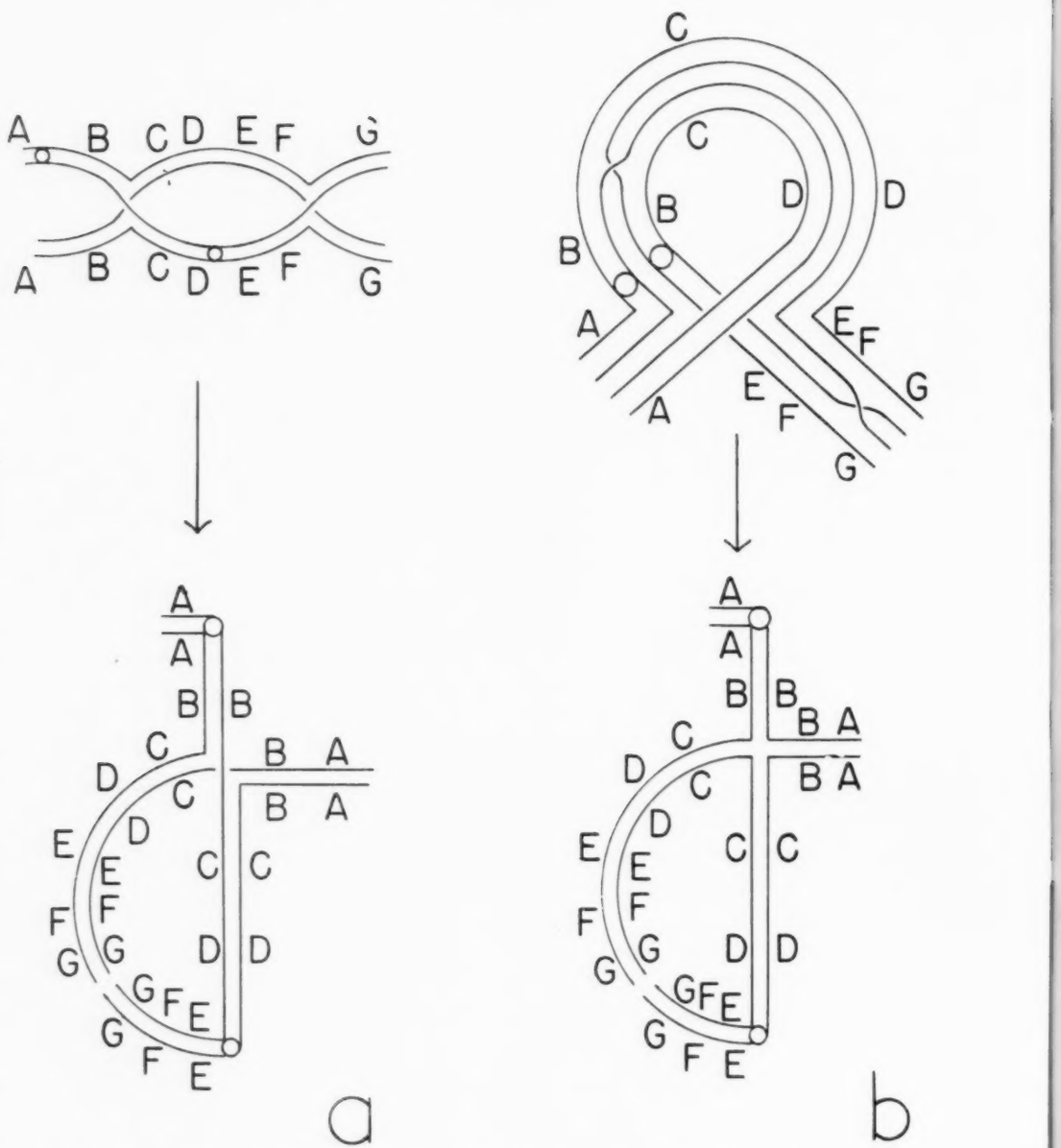

FIG. 7. Two different interpretations of the bivalent shown in figure 4 c. a, on the assumption that the bivalent is heterozygous for a pericentric shift; b, that it is heterozygous for a pericentric inversion.

Of the 12 rearrangements, one is in the X-chromosome and has only been found in the Cherry Creek population, while the remaining 11 are distributed over the nine "heteromorphic" pairs of autosomes. Not all these 11 autosomal rearrangements are, however, present in any one population, so far as we have been able to determine. The Whitewater population contains at least 7 and probably 8 of them, while 2 or 3 are absent from western Colorado, although common in the Great Basin populations.

It is extremely unfortunate that, of the nine heteromorphic autosomes, only one (No. 10, i.e. the next to the smallest autosome in order of size) can be invariably identified. The remaining 8 heteromorphic elements form a rather evenly graded series in respect of length, so that they can not be identified with certainty, although certain types of het-

TABLE 2. *Cytological characteristics of the populations collected in 1950*

Locality	Mean no. of heterozygous bivalents per individual	Mean no. of metacentric autosomes per individual	Mean no. of acrocentric autosomes per individual
Cedar Creek	1.16±.15	11.36	10.64
Olathe	1.06±.25	11.75	10.25
Delta	1.40±.25	11.40	10.60
Mack	1.26±.13	11.81	10.19
De Beque	1.17±.31	16.17	3.83
Rifle I	2.88±.44	12.12	7.88
Rifle II	1.33±.42	13.33	7.33
Piceance Creek	0.40±.24	8.40	11.60
Cortez	1.25±.21	11.81	10.19
Jensen	1.23±.12	11.57	10.43
Duchesne	1.92±.21	11.12	8.92
Delle	2.67±.29	10.09	11.91
Hinckley	2.57±.23	7.96	14.04
White Valley	1.82±.38	8.55	13.45
Robinson's Ranch	2.86±.34	10.29	11.71
Cherry Creek	2.29±.14	5.53	16.47
Railroad Valley	2.50±.27	10.05	11.95
Lovelock	3.00±.45	9.00	13.00
Rye Patch Dam	2.50±.20	10.64	11.36
Battle Mountain	2.45±.24	8.66	13.34

erozygous bivalents are quite characteristic, so that we can be sure that they are present in particular populations and absent in others. The data for the little 10th chromosome are accordingly given in table 6. We have omitted from this table the data on the Pojoaque population collected in 1949 because in this population chromosome 10 appears to be trimorphic rather than dimorphic, and is consequently very difficult to score accurately. Where a chromosome is trimorphic there will obviously be six different kinds of bivalents in the population, one of which will consist of two different types of metacentrics. Such a bivalent is illustrated in figure 4b (in an individual from Olathe). An exactly similar bivalent was encountered in one individual from Cortez.

As already stated (White, 1951) we do not know with absolute certainty whether the evolutionary changes from acrocentric to metacentric chromosomes which have occurred in the M.C. group of Oedipodine grasshoppers are pericentric inversions or shifts. This is a problem which can only be settled by a detailed study of pachytene pairing in squash-preparations of very high quality.

In a bivalent which consists of one acrocentric chromosome and one metacentric there are three different regions in which a chiasma may, theoretically, be formed. We call these the *short arm,* the *internal segment* and the *external segment* (fig. 6). Normally, in the structurally heterozygous bivalents of the M.C. grasshoppers chiasma-formation is restricted

TABLE 3. *Numbers of heterozygous bivalents per individual (eastern populations)*

	0	1	2	3	4	5	Heterozygous bivalents
Cedar Creek	6	16	7	2	—	—	31
Olathe	5	7	2	2	—	—	16
Delta	—	3	2	—	—	—	5
Mack	12	22	14	6	—	—	54
De Beque	1	3	2	—	—	—	6
Rifle I	—	1	2	3	1	1	8
Rifle II	1	3	1	1	—	—	6
Piceance Creek	3	2	—	—	—	—	5
Cortez	3	7	5	1	—	—	16
Jensen	4	21	8	2	—	—	35
Duchesne	3	6	10	4	3	—	26
11 m. SW. of Duchesne	—	1	1	—	—	—	2
Crescent Junction	—	—	2	—	—	—	2
Greenriver	—	—	1	—	—	—	1
Total	38	92	57	21	4	1	213

TABLE 4. *Numbers of heterozygous bivalents per individual (Great Basin Populations)*

	0	1	2	3	4	5	Heterozygous bivalents
Delle	1	3	6	4	6	1	21
Hinckley	—	3	10	5	4	1	23
White Valley	—	6	3	1	—	1	11
Robinson's Ranch	—	—	3	2	2	—	7
Cherry Creek	—	16	16	21	3	2	58
Railroad Valley	—	6	6	4	5	1	22
Lovelock	—	—	2	1	2	—	5
Rye Patch	—	2	5	5	2	—	14
Battle Mountain	1	6	10	5	5	2	29
Total	2	42	61	48	29	8	190

TABLE 5. *Supernumerary chromosomes*
V = Isochromosome supernumerary
S = Acrocentric supernumerary

	No. of individuals analyzed	Number with:			Total
		1S	1V	2S, 1V	
Eastern Populations					
Cedar Creek	31	—	—	—	—
Olathe	16	—	—	—	—
Delta	5	—	—	—	—
Mack	54	1	—	—	1
De Beque	6	—	—	—	—
Rifle I	8	—	—	—	—
Rifle II	6	—	—	—	—
Piceance Creek	5	—	—	—	—
Cortez	16	—	—	—	—
Jensen	35	—	—	—	—
Duchesne	26	1	—	—	1
11 miles SW. of Duchesne	2	—	—	—	—
Crescent Junction	2	—	—	—	—
Greenriver	1	—	—	—	—
Great Basin Populations					
Hinckley	23	—	1	—	1
White Valley	11	2	—	—	2
Robinson's Ranch	7	1	—	—	1
Delle	22*	—	1	—	1
Cherry Creek	58	2	1	1	4
Railroad Valley	22	2	2	—	4
Battle Mountain	29	4	—	—	4
Rye Patch Dam	14	1	1	—	2
Lovelock	5	—	—	—	—
	404	14	6	1	21

* One individual which could not otherwise be analyzed cytologically possessed an isochromosome supernumerary.

TABLE 6. *Data on chromosome 10*

	Homozygous acrocentric	Heterozygous	Homozygous metacentric
De Beque	—	2	4
Lovelock	1	3	1
Piceance Creek	3	2	—
Rifle II	2	2	2
Cortez	13	3	—
Rifle I	4	4	—
Battle Mountain	13	12	4
Rye Patch Dam	7	4	3
Olathe	12	4	—
Duchesne	16	10	—
Robinson's Ranch	1	6	—
Hinckley	13	9	1
Cedar Creek	24	6	1
Delta	3	2	—
Jensen	19	14	2
Delle	9	10	2
White Valley	8	2	1
Railroad Lake	4	13	5
Cherry Creek	32	21	5
Craig	55	15	3
Meeker	10	1	1
Whitewater	9	36	41
Mack	35	18	1
	293	199	77
		569	

to the external segment, and we formerly believed that chiasmata were never formed in the short arm or the internal segment. In the material from Battle Mountain, however, a structurally heterozygous bivalent which had a chiasma in the short arm (and none in the internal or the external segment) was found in a single cell of one individual (fig. 4, d). Also, in one individual from Cherry Creek, we found a structurally heterozygous bivalent in a single cell which apparently possessed two chiasmata, one in the internal segment and one in the external segment (fig. 4, c). The exact structure of this bivalent was not quite clear, and we are not sure which of the two interpretations (a or b) in figure 7 is correct. The uncertainty is unfortunate because if we had been able to analyze the chromatid configuration of this bivalent we would have solved the problem of whether the internal segments of the two homologs are mutually inverted or not (i.e. whether a pericentric inversion or a shift is present). In either case the presence of a chiasma in the internal segment would be expected to give rise to "lethal" gametes, but it is clear that the frequency of chiasma-formation in this "prohibited" internal region is extremely low (less than 1 in 10,000 cells) but not quite zero, as we formerly assumed. A chiasma in the short arm would not be expected to lead to any unfortunate consequences. The fact that a chiasma may be formed in the short arm of a structurally heterozygous bivalent proves that the rearrangements of the M.C. grasshoppers are not "terminal."

THE EASTERN POPULATIONS

Nine populations in western Colorado were sampled in 1950. Of these one (Cortez) is in southwestern Colorado, on McElmo Creek, a tributary of the San Juan river. Three others (Cedar Creek, Olathe and Delta) are in the Gunnison valley, four (Mack, De Beque, Rifle I and Rifle II) are in the Colorado valley, while one (Piceance Creek) is in the White River drainage basin, separated from the others by the Roan plateau and not far from Meeker, one of our former collecting stations (White, 1951). The samples from Cortez, Cedar Creek, Olathe and Mack are fairly adequate for determining the cytological composition of those populations, but the other samples each consist of less than 10 individuals and are hence of only limited value. Several days were devoted to collecting at De Beque, Rifle I, Rifle II and Piceance Creek, but the species was rare at all these localities.

The Cortez, Cedar Creek, Olathe, Delta and Mack populations do not seem to differ greatly from one another and will hence be considered together. In all these the chromosome number ($2N\,♂$) was found to be 23 and no supernumerary chromosomes were encountered except in one individual (out of 54) from Mack. The mean number of heterozygous bivalents ranges from 1.0 to 1.4 in these populations, the greatest number of heterozygous bivalents observed in a single individual being three (it is probable that if the samples had been larger some quadruple or quintuple heterozygotes would have been observed). In all of these populations

except the one from Delta (where the sample only consisted of 5 individuals) a significant percentage of the individuals (19% to 31%) were structural homozygotes. The mean number of metacentric autosomes ranges from 11.35 at Cedar Creek to 11.88 at Cortez, the differences between the means of the various populations being non-significant.

It will be evident that these five populations are very similar in cytological constitution and that they differ very profoundly from the sample collected at Whitewater in 1949 (White, 1951). The principal difference consists in the fact that at Whitewater the mean number of metacentric autosomes is approximately 19.05. This difference in the mean number of metacentric autosomes is particularly surprising since the Whitewater locality is only about 19 miles from "Delta" and 34 miles from "Mack" (as shown in table 1, the collecting localities were actually some distance from the towns bearing those names). We must therefore conclude that the Whitewater area is inhabited by a peculiar "microgeographic race" characterized by a much higher number of metacentric chromosomes than the populations higher up the Gunnison valley and below it, in the main valley of the Colorado. Most of the territory between Delta, Whitewater and Mack seems eminently suitable for *T. sparsa* (except where cultivated fields or orchards are present) and we have no doubt that numerous colonies of the species exist between these localities. The microgeographic race found at Whitewater appears to be also present at De Beque, approximately 33 miles to the northeast, where a sample of six individuals showed a mean number of 16.17 metacentric chromosomes. All these six individuals were, however, homozygous for the chromosomal fusion previously mentioned, which was not present in any of the 86 individuals from Whitewater. We formerly (White, 1951) suggested that the Roan plateau might have formed a barrier to the spread of this fusion southward. It is now clear that this is not so; the main distribution area of the fusion is undoubtedly to the north of the Roan plateau, where it has been found in the Craig, Meeker, Piceance Creek and Duchesne populations (but not in the Jensen population). It was, however, encountered in the homozygous state in all the six individuals from De Beque, in the eight from Rifle I and in four of the six from Rifle II (these three localities being all south of the Roan plateau). No individuals heterozygous for the fusion have been found in Colorado, but at Duchesne, Utah, 24 individuals possessed the fusion in the homozygous state, one lacked it entirely and one was heterozygous for it. The latter individual showed a characteristic trivalent composed of two J-shaped elements paired with the arms of a metacentric V at the first meiotic division (fig. 4, a). We have previously (White, 1951) suggested that such individuals, if they occurred, might show some degree of sterility, due to occasional mal-orientation of the trivalent on the first meiotic spindle. Unfortunately the single fusion heterozygote found in the Duchesne population did not show many first meiotic divisions, so that the hypothesis could not be tested. But W. L. Evans (unpublished) who has investigated a similar case in *Circotettix undulatus* has found that mal-orientation of the trivalent is not infrequent in fusion-heterozygotes of that species.

The samples from Rifle I, Rifle II and Piceance Creek, although very small, are interesting on account of the very great differences in the mean number of heterozygous bivalents. The localities we have called Rifle I and Rifle II are only about six miles apart, and are not separated by any terrain which appears unsuitable for the species. The Piceance Creek locality lies about 18 miles northwest of Rifle I and is separated from it by the Roan plateau, on which we have searched for *T. sparsa* in vain and which seems ecologically unsuited for the species. The Piceance Creek population, with a mean of 0.4 heterozygous bivalents per individual (on the basis of only 5 individuals) shows the lowest degree of structural heterozygosity of any of the populations hitherto studied. Rifle I, on the other hand, shows a very high degree of heterozygosity (mean = 2.88). At Rifle II the degree of heterozygosity (mean = 1.33) seems to be approximately "normal" for western Colorado. Both at Rifle I and Rifle II the mean number of metacentric bivalents is lower than at De Beque and Whitewater, but higher than in the populations to the north of the Roan plateau (Piceance Creek, Meeker and Craig). Thus in this respect (and in this respect only) Whitewater, De Beque, Rifle I and II and the localities to the north of the Roan plateau seem to represent points on a cline.

Turning to the two localities in northeastern Utah, we find that the population at Jensen resembles those at Mack, Delta, Olathe, Cedar Creek and Cortez in its degree of heterozygosity, in the mean number of metacentric chromosomes and in apparently lacking supernumeraries. Rather surprisingly this population also seems to lack the chromosomal fusion present at Duchesne, about 64 miles away. The Duchesne population is remarkable in being one of the two in which some individuals possess the fusion while others lack it (the other being Rifle II) and also in having a significantly higher degree of heterozygosity than any of the other "Eastern" populations except Rifle I.

The Great Basin Populations

The samples collected in western Utah and northern Nevada differ cytologically from those in western Colorado in showing a much greater degree of structural heterozygosity. With the exception of the Cherry Creek population, which is anomalous in several respects, the other Great Basin samples are cytologically rather similar, so that they can be treated together. The mean number of heterozygous bivalents per individual ranges from 1.82 at White Valley to 3.00 at Lovelock. All of these populations have $2N\,♂ = 23$, i.e. none of them possess the chromosomal fusion present in area A (fig. 1). Structural homozygotes seem to be almost absent from the Great Basin area. Out of 190 individuals only two were classified as homozygotes (table 4) and one of these may have been heterozygous for a rearrangement which is very difficult to detect (i.e. a shift of the centromere through a very short distance). The mean number of metacentric chromosomes per individual (table 2) ranges from 5.53 at Cherry Creek to 10.64 at Rye Patch Dam, i.e. it is generally lower than in the eastern populations.

Whereas in the Eastern populations the three longest chromosome pairs (nos. 1, 2, 3) seem to be invariably metacentric, in the Great Basin populations one or two of these elements are heteromorphic. This is particularly clear in the Cherry Creek population in which only one chromosome (probably no. 1) is invariably metacentric.

This Cherry Creek population is unique in several respects. In the first place the mean number of metacentric autosomes (5.53) is lower than in any of the other populations sampled. If we could be certain that all evolutionary changes in chromosomes shape in this species were in the direction acrocentric $\longrightarrow$ metacentric, we might say that the Cherry Creek population was the most "primitive" one studied, the Whitewater population being the most "advanced." Now it is certain that the members of the M.C. group are descended from ancestral forms in which all the chromosomes were acrocentric. But this does not necessarily imply that the evolution of chromosome form in such species of section B as *T. sparsa* has been exclusively uni-directional (i.e. changes from the metacentric form to the acrocentric may also have taken place, by structural rearrangement, from time to time).

In the second place, the Cherry Creek population is the only one we have studied in which the X-chromosome is not invariably metacentric. Of 58 male individuals studied 32 had the X metacentric, while in the remaining 26 it was acrocentric. The conclusion seems inevitable that nearly half the females must have the XX chromosome pair structurally heterozygous. The combined length of the two chromosome arms in the metacentric type of X is approximately equal to the length of the acrocentric type. Here again we are confronted with a dilemma: does the acrocentric type of X at Cherry Creek represent the primitive condition, still present in the species belonging to section A or does it represent an "evolutionary reversion" which has taken place, by structural rearrangement, in this part of Nevada and has not spread to other areas in which the species occurs?

With a single exception, all the other M.C. grasshoppers which have been studied (17 species altogether) invariably possess a metacentric X. The exception is *Trimerotropis gracilis*, which normally has the X metacentric, but in which we have found two populations (one at Lucky Boy Pass, Mineral Co., Nevada, the other near Soldier Summit in central Utah) which resemble the Cherry Creek population of *sparsa* in showing both acrocentric and metacentric X's.

The simplest explanation of these facts would seem to be that at a very early stage in the evolutionary history of the M.C. group the X became metacentric and that this condition has been retained in all the descendants of this phyletic line, except that in *sparsa* and *gracilis* structural rearrangements have occurred which converted the X once more into an acrocentric, these rearrangements being confined to relatively small parts of the total geographic range of those species.

Discussion

Our studies on *Trimerotropis sparsa* present a picture of a species with an extremely complex cytogenetic system, broken up into a number of microgeographic races, each with its own system of cytological polymorphism. Such a situation would hardly be possible in a migratory species in which large numbers of individuals were frequently exchanged between populations. The cytological evidence thus confirms the view that *Trimerotropis sparsa,* probably in common with most other species of the genus, is an extremely sedentary insect, restricted to certain rather specialized habitats, and that the home-range of the individuals is extremely small. At the time when we wrote our former paper (White, 1951) it was not clear whether or not differences in cytological composition existed only between populations isolated by some geo-

graphical barrier such as a mountain range. It is now certain that such differences may exist between populations less than 20 (and probably less than 10) miles apart which are not separated by any geographic or ecological barrier to the spread of the species.

Our survey of the cytological composition of the populations of *Trimerotropis sparsa* may be compared with that carried out on the populations of *Drosophila willistoni* in Brazil by Da Cunha, Burla and Dobzhansky (1950). *D. willistoni* shows a higher degree of chromosomal polymorphism than any other species of *Drosophila* hitherto studied, due to the presence of about 40 different inversions, distributed over the five chromosome arms. The amount of structural heterozygosity is especially high in central Brazil and seems to show a general tendency to decrease towards the periphery of the distribution area of the species, although some populations are exceptional in this respect and the exact limits of the distribution of *D. willistoni* are not known with any accuracy.

Da Cunha, Burla and Dobzhansky interpret their results as indicating that the variety of ecological niches or habitats occupied by *D. willistoni* is greatest in the center of its range. They further believe that "the amount of chromosomal polymorphism, and in general the amount of adaptive genetic variability, is proportional to the variety of habitats which the species has mastered in the environment of a given region."

These concepts do not seem to fit the case of *Trimerotropis sparsa* particularly well. We believe that the limits of distribution of the species are shown with a fair degree of accuracy in figure 1, but within the line which indicates those limits there are certainly areas (such as the central mountain ranges of Utah and the higher parts of the Rocky Mountains in Wyoming and Montana) from which the species is entirely absent. Should one consider localities on the edge of these "uninhabited" areas "peripheral" in the sense of Da Cunha, Burla and Dobzhansky? In any case we can see no evidence that the variety of different types of habitats available to *T. sparsa* decreases towards the periphery of its range. In western Colorado the variety of habitats, in the valleys of the Colorado and Gunnison rivers and on the lower edge of the transition zone above the valley floors, is certainly much greater than in the Great Basin, where the species seems to be confined to the very uniform environment of Sarcobatus flats. In spite of this the amount of structural heterozygosity is much greater in the Great Basin populations than in those from western Colorado. It is, of course, conceivable that the climatic conditions vary more from year to year at any one locality in the Great Basin than they do in western Colorado.

Even on the assumption that the chromosomal polymorphism of *T. sparsa* is adaptive (an assumption which, as already pointed out, is still unproven) we may assume either that the cytological differences between the various populations are mainly adaptive or mainly due to historical accident. In the former case the relative uniformity of the cytological composition of the Great Basin populations would be due to the environment of the different playas being fundamentally similar (with the Cherry Creek playa anomalous in some way); while in the latter case it would be due to their having had a similar history, the Cherry Creek population having had a somewhat different history. In view of the fact that the Great Basin must have possessed a much wetter climate during the late Pluvial period, only a few thousand years ago, it is possible that this species of extremely arid sunbaked areas is a relative newcomer in that region, and may have existed for a much longer time in the Colorado drainage basin farther east. If so, that might account for the fact that it has not broken up into many microgeographic races in the Great Basin in the way that it has done in western Colorado and eastern Utah.

Dobzhansky (personal communication) has suggested that cytological polymorphism may be reduced even in an area which contains a large variety of different habitats if many of these are occupied by other, competing species. It is almost certain that the shadscale zone in western Colorado supports more different species of grasshoppers than the Sarcobatus playas of the Great Basin, but in the absence of exact information on the extent to which the various species are competing with *T. sparsa* the significance of this fact is difficult to estimate. At Mack, where the degree of heterozygosity was relatively low, *T. sparsa* was by far the commonest species, the few other forms represented in the grasshopper fauna being relatively scarce.

The fact that chiasmata are almost never formed in the internal segment of the structurally heterozygous bivalents of the M.C. grasshoppers means, of course, that structural heterozygosity is acting as an effective cross-over suppressor, just as in the case of inversions in *Drosophila* species. There is accordingly the physical basis for the development of genic as well as structural polymorphism on a very large scale. Unfortunately, we have no means of proving the existence of this genic diversity and, even if it exists, the exact role that it plays in the population-dynamics of *T. sparsa* (and other species having the same type of cytological mechanism) is still mysterious, although one must strongly suspect that some kind of heterosis is involved.

Our material of *T. sparsa*, consisting of about 900 individuals from 29 different localities, exhibits a considerable amount of variation in external morphology, which we intend to deal with in a later paper. We have no reason to believe, however, that more than one species is involved. Whereas the eastern forms of *T. sparsa* and *T. gracilis* (i.e. those from Colorado and northern New Mexico) are amply distinct, material of the two species from Nevada may be hard to separate and we believe that the two species are much more closely related than would be suspected if one were only familiar with their eastern races. Even in Nevada, however, the two species may be distinguished by the form of the metazonal carina and certain characters of the ovipositor valves. In addition, all the populations of *gracilis* that we have studied possess a chromosomal fusion, such as is only present in area "A" of the distribution of *sparsa*.

There is some evidence that individuals from populations which are cytologically anomalous are also atypical in external morphology (e.g. at Whitewater the fastigium is unusually narrow in both sexes).

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Summary

Twenty-seven populations of the grasshopper *Trimerotropis sparsa* collected in New Mexico, Colorado, Utah and Nevada all contained individuals structurally heterozygous for chromosomal rearrangements involving a change in the position of the centromere. Such heterozygotes greatly outnumber the homozygotes, and many populations consist almost entirely of structural heterozygotes. At least 12 different chromosomal rearrangements are responsible for the cytological polymorphism of this species. Many of these rearrangements seem to be widespread, but some of them have a restricted distribution. The X-chromosome is normally metacentric, but an acrocentric type of X was also found in one population (Cherry

Creek, Nevada). A chromosomal fusion is present in northwestern Colorado and in a small area of eastern Utah. Supernumerary chromosomes are present in some individuals in most of the populations studied, but are absent from a fairly large area of western Colorado. These supernumeraries are of two types, one kind being acrocentric, the other kind metacentric. The latter are isochromosomes, whose arms pair together at meiosis.

It is believed that the chromosomal polymorphism of *T. sparsa* and related species is adaptive and probably furnishes the physical basis for a genetic mechanism leading to heterosis, but no definite proof of this has yet been obtained.

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MODIFICATION OF THE ADAPTIVE VALUES OF CHROMOSOMAL TYPES IN *DROSOPHILA PSEUDOOBSCURA* BY NUTRITIONAL VARIABLES

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INTRODUCTION

Most natural populations of *Drosophila pseudoobscura* are polymorphic with respect to the gene arrangement in some of the chromosomes, especially the third chromosomes. Some of the wild flies are inversion heterozygotes and others are homozygotes. It has been shown both through observations on natural populations, and through experiments on artificial ones that the chromosomal polymorphism is adaptive and balanced (Wright and Dobzhansky, 1946; Dobzhansky and Levene, 1948). In at least some environments the adaptive values of inversion heterozygotes are higher than those of the homozygotes. However, the adaptive values of chromosomal types can easily be modified by environmental factors. In experiments conducted at 25° C., the adaptive value of heterozygotes for Standard and Chiricahua third chromosomes for certain California populations is about twice as high as that of the Chiricahua homozygotes; at 15° C. these chromosomal types are similar in adaptive value. Heuts (1947, 1948) found that the relative humidity may also modify the adaptive values. Heuts (l.c.) and Wallace (1948) showed that the adaptive value of a chromosomal type is a resultant of interaction of many physiological variables: The ability of larvae to survive under competition for a limited amount of food, fecundity, longevity, sexual activity, etc. Furthermore, a chromosomal type may be superior to another type in some of these properties, equal in others, and inferior in still others. The chromosomal types possess different ecological optima.

Perhaps the least well known, and yet doubtless very important, variables of Drosophila ecology are those concerned with the nutrition of the flies. Dobzhansky and Epling (1944) and Shihata (unpublished) found that adult *D. pseudoobscura* caught in their natural habitats contain yeasts and bacteria in their digestive organs. Shihata has isolated 32 species of yeasts from 92 flies collected in 5 localities in California. Carson (1951) found both adults and larvae feeding in slime fluxes on diseased oaks and other trees. Considerable differences in the nutritional values of different yeasts have been found by Burkholder (1943a and b), Christophersen and Holzweissig (1950), Hedrick and Burke (1950), and others. Wagner (1944, 1949) found that certain species of yeasts permit normal development of some but not of other species of Drosophila related to *D. mulleri*. Experiments on the influence of different species of yeasts and bacteria in the food on the adaptive value of the chromosomal types of *D. pseudoobscura* are reported in the present article.

MATERIAL AND TECHNIQUE

Experimental populations of *Drosophila pseudoobscura* were kept in population cages of a type described by Wright and Dobzhansky (1946) and Dobzhansky (1947). Stender jars with the cream of wheat and molasses medium (Spassky, 1943) were inoculated with desired species of microorganism and inserted into the population cages. The Drosophila populations were mixtures of two gene arrangements in the third chromosome, namely Standard (to be referred to below as ST) and Chiricahua (CH). At appropriate intervals, samples of the eggs deposited by the flies in the population

cages were taken, the larvae hatching from them were raised under optimal conditions in regular culture bottles, and their salivary gland chromosomes were examined in smear preparations stained with acetic orcein. For a more detailed description of the technique of sampling the chromosomes in the population cages, see Wright and Dobzhansky (1946).

The flies used in the experiments are descendants of ancestors collected at Piñon Flats, Mount San Jacinto, California. The 12 different strains homozygous for the ST and an equal number of strains homozygous for CH chromosomes which were used in the experiments to be described are the same as used previously by Dobzhansky (1949). A total of 9 species of yeasts and 2 bacterial cultures were used. Among these, 4 yeasts and the bacteria were isolated in 1946 and 1947 by Dr. R. P. Wagner at Piñon Flats, California, and the remainder by Dr. A. El Tabey Shihata at Keen Camp, California, in 1950. All of these microorganisms were found in the crops of *Drosophila pseudoobscura* flies collected in the above localities. The technique of isolation of microorganisms from fly crops has been described by da Cunha, Dobzhansky, and Sokoloff (1951). The writer is deeply obliged to Drs. E. M. Mrak, H. Phaff, and A. El Tabey Shihata for the determination of the species of the yeasts used.

The following technique has been used for feeding the experimental populations. Inocula of the microorganisms were introduced daily into 500 cc. Ehrlenmeyer flasks, containing 100 cc. of nutrient media. The medium for the yeast consisted of 50 gr. of dextrose, 12.5 gr. of malt extract broth (Difco), and 6.7 gr. of yeast nitrogen base (Difco) in one liter of water. The medium for the bacteria consisted of 8 gr. of nutrient broth (Difco) in 1 liter of water. The cultures were left standing for about 24 hours at room temperature, and for 24 hours on a shaker at 25° C. Subsequent to this, the cultures were centrifuged, the supernatant decanted, and the residue resuspended in distilled water. Stender jars with Drosophila food medium were sterilized in an autoclave, inoculated with a suspension of a desired microorganism, and left standing for at least 4 days in a sterilized jar at room temperature. A good growth of the microorganism develops on the food medium during this time, whereupon the jars are introduced into the population cages. In the cages kept at 25° C. a new jar was introduced on alternate days, and in those kept at 16½° C. at 4 day intervals.

The initial populations of the flies in the experimental cages were raised in regular culture bottles with Fleischmann's yeast. But, before being placed into the cages, the flies were transferred 5 to 6 times at daily intervals into culture bottles with a heavy growth of the microorganism on which they and their offspring were to feed in the population cages. The intestinal flora of the flies was thus made to consist of the desired species of microorganism, since, as shown by Dobzhansky and Epling (1944) and by Shihata (unpublished) the fly crop is emptied of its contents in less than 48 hours at 25° C. The population cages are maintained for several months, and there is no doubt that the food in them becomes eventually infected by bacteria and by mold spores. The infection by foreign species of yeasts is quite unlikely. Since the food medium in the population cages tends to become dry, it is irrigated daily by the suspension of the desired microorganism in water. The suspension is introduced by means of a previously sterilized glass tube. The writer is fully aware that the food in the population cages contained more than a single species of microorganisms. Nevertheless, it is certain that the Stender jars when introduced into the cages contained only the desired microorganism species which had a head start in growth. The irrigation of the food certainly maintained that species always predominant, or at any rate frequent, in the food taken by the adult flies and the larvae in the population cages.

The average length of a fly generation in the experimental cages is estimated to have been 3.9 weeks at 25° C. At 16½° C. the development rate varied somewhat in different experiments, but for the purposes of the calculations it is taken to be 8 weeks on the average. Samples of the populations were taken at approximately monthly intervals. On six consecutive days, jars with food were introduced into the cages, some of the eggs deposited on them were transferred into regular culture bottles, and the larvae hatching from these eggs were allowed to develop under optimal conditions. Twenty-five larvae from each of the six cultures were examined cytologically. Thus the monthly sample consisted of 150 larvae, and since a larva has two third chromosomes, the gene arrangement was determined in 300 chromosomes. In tables 1 and 2, only the frequencies of ST chromosomes are given, the remainder being CH chromosomes. Since the frequency is based on 300 observations, the standard errors of these frequencies are between 0.021 and 0.029 (2.1 to 2.9 per cent).

Experiments of 1949–1950

In the experiments Nos. 1, 4, 5, and 6, the initial population of each cage consisted of 330 virgin ♀♀ and 330 ♂♂ homozygous for the CH gene arrangement, and 165 virgin ♀♀ and 165 ♂♂ homozygous for the ST chromosomes. The initial frequency of ST chromosomes in these populations were, accordingly, 33.3 per cent, and of CH chromosomes 66.7 per cent. The parent flies belonged to strains homozygous for individual third chromosomes, raised in regular culture bottles. It happened that the CH homozygotes, or some of them, were much weaker, or less fertile, than a majority of ST homozygotes. For this reason, the first generation which developed in the cage often contained a great excess of ST chromosomes. Since our purpose is to study the selective process in panmictic populations, in which many individuals are ST/CH heterozygotes, and the ST/ST and CH/CH individuals usually carry two chromosomes of different origin, the changes observed during the first generation in the population cages had little meaning. This first generation was, accordingly, ignored in the calculations presented below.

Experiments of 1950–1951

In the experiments Nos. 7–18, the initial population of each cage consisted of about 2000 ♀♀ and ♂♂, which were F_1 hybrids between ST and CH strains. These flies were raised in regular culture bottles, care being taken that all 12 ST and 12 CH strains should be about equally numerous in the foundation stock. Here, then, the eggs deposited in the population cages by the introduced flies consisted of necessity of 25% ST homozygotes, 50% ST/CH heterozygotes and 25% CH homozygotes. The initial gametic frequencies of ST and CH chromosomes were 50%. The structural homozygotes, ST/ST and CH/CH, carried chromosomes of different origin, and had, accordingly, a normal amount of hybrid vigor. All the changes observed in such populations are meaningful for our purposes.

Rhodotorula mucilaginosa

This yeast has been isolated by Dr. Wagner at Piñon Flats, California, in 1947, and was used in the experiment No. 53 of Zimmering and Dobzhansky (Dobzhansky, 1948, p. 199). Two more experiments, Nos. 1 and 11, were carried out in 1949–1950, and the results are shown in table 1. Experiment No. 1 was started with a population consisting of 33.3% of ST and 66.7% of CH flies, but, for reasons stated above, the initial frequency must be regarded as that reached in early November, 1949, i.e., 64% of ST chromosomes. Similarly, the initial frequency in the Zimmering and Dobzhansky experiment is taken to be 46.3% of ST chromosomes. In all experiments the frequencies of ST chromosomes rose at the expense of CH, but none of the experi-

TABLE 1. *Frequencies of Standard third chromosomes, observed in experimental populations fed on different microorganisms. Experiments of 1949–1950.*
E = early; M = middle; L = late

Time	Experiment 1 *Rhodotorula mucilaginosa*	Experiment 4 *Bacteria No. 3*	Experiment 5 *Bacteria No. 9*	Experiment 6 *Zygosaccharomyces dobzhanskii*	Experiment 7 *Zygosaccharomyces dobzhanskii*	Experiment 8 *Saccharomyces cerevisiae*	Experiment 9 *Torulopsis* sp.	Experiment 10 *Candida parapsilosis*	Experiment 11 *Rhodotorula mucilaginosa*
E October '49	0.333	0.333	0.333	0.333	—	—	—	—	—
E November '49	0.640	—	—	0.610	—	—	—	—	—
M November '49	—	0.573	0.587	—	—	—	—	—	—
M December '49	0.663	—	—	0.688	—	—	—	—	—
L December '49	—	0.723	0.790	—	—	—	—	—	—
L January '50	—	—	—	—	0.500	0.500	0.500	—	—
M February '50	—	0.833	0.797	—	—	—	—	0.500	0.500
M March '50	—	—	—	—	0.703	0.690	0.677	—	—
L March '50	—	—	0.870	—	—	—	—	—	—
E April '50	—	0.810	—	—	—	—	—	0.533	—
M April '50	—	—	—	—	—	0.687	0.699	—	0.600
E May '50	—	—	0.873	—	0.790	—	—	—	—
M May '50	—	0.877	—	—	—	—	—	0.650	—
L May '50	—	—	—	—	—	0.677	—	—	0.640
E June '50	—	—	—	—	—	—	—	0.660	—

TABLE 2. *Frequencies of Standard third chromosomes, observed in populations fed on different microorganisms. Experiments of 1950–1951.* E = early; M = middle; L = late.

Time	Experiment 14 *Zygosaccharomyces dobzhanskii*	Experiment 15 *Zygosaccharomyces drosophilae*	Experiment 16 *Kloeckeraspora apiculatus*	Experiment 17 *Candida guilliermondii*	Experiment 18 *Candida krusei*
L September '50	0.500	0.500	0.500	0.500	—
E October '50	—	—	—	—	0.500
E November '50	0.667	0.673	—	—	—
M November '50	—	—	0.610	0.603	0.723
E December '50	0.690	0.670	—	0.667	—
M December '50	—	—	0.643	—	0.737
E January '51	0.753	0.760	—	0.723	—
M January '51	—	—	0.757	—	0.773
E February '51	0.783	0.730	—	0.700	—
M February '51	—	—	0.820	—	0.767

ments were continued long enough for the populations to reach the equilibrium proportions of the two kind of chromosomes.

The calculations of the adaptive values of the ST/ST and CH/CH homozygotes and ST/CH heterozygotes were made with the aid of the method of Wright and Dobzhansky (1946). The adaptive value of the heterozygotes is arbitrarily taken to be unity; those of the ST/ST and CH/CH homozygotes then turn out to be 0.83 and 0.49 respectively (table 3). From these values, the equilibrium frequency of ST chromosomes may be calculated to be $\hat{g} = (1 - 0.49)/(1 - 0.49 + 1 - 0.83) = 0.75$. This is reasonably close to the final value, 0.70, observed in the experiment of Zimmering and Dobzhansky.

Zygosaccharomyces dobzhanskii

The yeast has been isolated by Dr. Wagner at Piñon Flats, and described by Dr. Shihata. It was used in the experiment No. 54 of Zimmering and Dobzhansky (Dobzhansky, 1948, p. 199), and in the experiments Nos. 6, 7, and 14, reported in tables 1 and 2. The initial frequency given by Dobzhansky, as well as that in the experiment No. 6, were disregarded in making the calculations of the adaptive values. The changes observed in the population cages with the yeast are considerably more rapid than those in cages fed on *Rhodotorula*. In the experiment of

TABLE 3. *Estimates of the adaptive values of the chromosomal types, and of the equilibrium frequencies of the Standard and Chiricahua chromosomes, in the experimental populations*

Food	Adaptive value (W)			Frequency at equilibrium (♀)	
	ST/ST	ST/CH	CH/CH	ST	CH
Saccharomyces cerevisiae (Fleischmann's yeast)	0.71	1	0.32	0.70	0.30
Rhodotorula mucilaginosa	0.83	1	0.49	0.75	0.25
Candida parapsilosis	0.89	1	0.54	0.80	0.20
Zygosaccharomyces dobzhanskii	1.06	1	0.35	1.00	0.00
Zygosaccharomyces drosophilae	<1	1	<1	±0.73	±0.27
Kloeckeraspora apiculatus	1.55	1	1.00	1.00	0.00
Candida guilliermondii	0.80	1	0.32	0.77	0.23
Candida krusei	<1	1	<1	±0.75	±0.25
Bacteria No. 3	1.14	1	0.37	1.00	0.00
Bacteria No. 9	1.15	1	0.57	1.00	0.00

Zimmering and Dobzhansky the frequency of ST chromosomes ran from 0.55 to 0.90 in about four and a half months. The calculations of the adaptive values (table 3) disclose that the ST/ST homozygotes are superior to the CH/CH homozygotes (0.35) as well as to the ST/CH heterozygotes. In other words, the heterozygotes show no heterosis in the populations fed with this yeast. Theoretically, this should lead eventually to the elimination of CH by natural selection, but none of our populations were maintained long enough for such elimination to be observed.

Zygosaccharomyces drosophilae

This yeast was isolated by Dr. Shihata at Keen Camp, California, in 1950. Only a single population, No. 14 was fed on this yeast (table 2). The frequency of ST chromosomes rose very sharply from the initial 0.50 to 0.67, but an equilibrium was reached between 0.70 and 0.75. The data are insufficient to calculate the adaptive values of the chromosomal types, but it is possible to tell that the ST/CH heterozygotes exhibit a strong heterosis.

Torulopsis sp.

The yeast was isolated by Dr. Wagner at Piñon Flats. Only a single experiment, No. 9, reported in table 1, has been made with this yeast. The data are insufficient for calculation of the adaptive values of the chromosomal types, but the ST/CH heterozygotes seem to be superior to the homozygotes.

Candida parapsilosis

Isolated by Dr. Shihata at Keen Camp, California in 1949. This yeast was used in the experiment No. 10 (table 1). The observed changes in the frequencies of the chromosomal types yield the estimates 0.89 and 0.54 for the adaptive values of the ST/ST and CH/CH homozygotes respectively. From these values, the equilibrium frequency of ST chromosomes is expected to be about 0.8, which is considerably higher than reached in the experiment. Since, however, the experiment was carried only for three and a half months, this result is not surprizing.

Candida guilliermondii

Isolated by Dr. Shihata at Keen Camp in 1950, and used in the experiment No. 17, reported in table 2. The frequency of ST chromosomes rose rather gradually from 0.5 to about 0.7. The data suggest that the adaptive value of the CH/CH homozygotes is very low, about a third of that of the heterozygotes.

Candida krusei

Isolated by Dr. Shihata at Keen Camp in 1950, and used in the experiment No. 18, reported in table 2. The frequency of ST chromosomes rose very steeply from 0.5 to about 0.75 within about two months, and then did not increase much for the following three months. The data do not yield self-consistent estimates of the adaptive values, but it can be stated that the ST/CH heterozygotes growing on this yeast are strongly heterotic. In other words, the adaptive values of both homozygotes are very low compared to that of the heterozygote.

Kloeckeraspora apiculatus

Isolated by Dr. Shihata at Keen Camp in 1950, and used in the experiment No. 16, reported in table 2. The frequency of ST chromosomes was rising steadily during the five months during which this experiment continued. The chromosomal types show a unique set of adaptive values when developing on this yeast. Namely, the adaptive values of the CH/CH homozygotes and the ST/CH heterozygotes are alike within the limits of the experimental error, while the ST/ST homozygotes are distinctly superior to the other two types. The heterosis is, thus, definitely absent.

Bacteria, Strain No. 3

Isolated by Dr. Wagner at Piñon Flats in 1946. The culture was lost before an examination of the organism could be

made. This culture was used in the experiment No. 4 (table 1). The frequency of ST chromosomes rose very rapidly, from 0.57 to 0.72 in about 6 weeks, and then more slowly to 0.88 about four and a half months later. The adaptive values calculated from these dates are 1.14 for ST/ST homozygotes and 0.37 for CH/CH homozygotes. It follows that in this experiment, like in that involving *Zygosaccharomyces dobzhanskii*, the adaptive value of the heterozygote is intermediate between those of the homozygotes, i.e., no heterosis is observed.

Bacteria, Strain No. 9

Isolated by Dr. Wagner, simultaneously with No. 3. When examined in March of 1951 by Mrs. Lillian Schneider, the culture proved to be a mixture of two distinct organisms, one of which was, however, almost 1,000,000 times more numerous than the other when grown on the Drosophila culture medium. The predominant organism belongs probably to the genus *Erwinia;* the rare organism belongs probably to *Alcaligenes.*

The experiment No. 5 (table 1) in which the strain 9 was used to feed the flies gave results very similar to those obtained with the strain 3. The adaptive value of ST/ST homozygotes turns out to be 1.15 and of CH/CH homozygotes 0.57. The heterozygotes have, of course, the adaptive value of unity. No heterosis is present.

EXPERIMENTS AT 16° C. TEMPERATURE

All the experiments described above have been carried at 25° C. Wright and Dobzhansky (1946) showed however that the adaptive values of the chromosomal types are very sensitive to temperature variations. At 25° C., and with Fleischmann's yeast, the carriers of the different chromosomal types are very different in adaptive value. Yet, at 16° C., the chromosomal types are so nearly alike in adaptive value that no selective changes can be detected within several generations. In 1949–1950, two populations, fed on *Rhodotorula mucilaginosa* and on *Zygosaccharomyces dobzhanskii* respectively, were kept at 16° C. The experiments were started with 33.3 per cent ST and 66.7 per cent CH chromosomes, but, for reasons stated above in the description of the 1949–1950 experiments at 25° C., the changes observed between October 1949 and January 1950 (table 4) are meaningless for our present purpose. No significant change has taken place in the population fed on *Rhodotorula* between January and May, 1950. The population fed on *Zygosaccharomyces* showed, on the contrary, a quite significant increase in the frequency of ST chromosomes (table 4). In 1950–1951, two more populations were kept at 16° C., and fed on *Zygosaccharomyces dobzhanskii* and on the bacterial strain No. 9 respectively. In both populations significant increases in the frequencies of ST chromosomes have been observed (table 4). It may be recalled that both *Zygosaccharomyces* and the bacteria confer very high selective advantages on ST/ST homozygotes also at 25° C. (table 3). The uniformity of the adaptive values of the chromosomal types observed at 16° C. by Wright and Dobzhansky (1946) obtains, accordingly, only with

TABLE 4. *Frequencies of Standard third chromosomes observed in populations kept at a low temperature (16° C.).*
E = early; M = middle; L = late

Time	Experiment 2 *Rhodotorula mucilaginosa*	Experiment 3 *Zygosaccharomyces dobzhanskii*
E October '49	0.333	0.333
M January '50	0.557	0.533
L March '50	0.517	0.637
L May '50	0.557	0.640
	Experiment 13 *Bacteria No. 9*	Experiment 12 *Zygosaccaromyces dobzhanskii*
L September '50	0.500	0.500
L December '50	0.627	0.650
L January '51	0.586	0.580
L March '51	0.630	0.613

some microorganisms used for food, while a differentiation of the adaptive values occurs on other foods.

Discussion

The data presented above show that the relative adaptive values of the homo- and heterozygotes for the ST and CH gene arrangements in *Drosophila pseudoobscura* vary greatly depending upon the species of yeast or bacteria which serve as food for the flies and their larvae. It is particularly significant that while the heterozygotes usually show an adaptive superiority (heterosis) over the homozygotes, at least two species of yeast and the bacteria used in our experiments caused the adaptive value of the heterozygotes to fall below that of ST homozygotes. Compared to the result obtained by Wright and Dobzhansky (1946) and Dobzhansky (1947, 1949) with populations fed on Fleischmann's yeast (*Saccharomyces cerevisiae*), some of the microorganisms used in the present experiments have increased, while others have decreased, the disparities between the adaptive values of the chromosomal types (see table 3).

The nutritional requirements of *D. melanogaster* include at least the vitamins B_1, B_2, B_6, nicotinic acid, pantothenic acid, biotin, folic acid, cholesterol, and nucleic acid (Chu, 1935; van't Hoog, 1936; Lafon, 1937; Tatum, 1941; Schultz *et al.*, 1946; and Begg and Robertson, 1950). Different species and strains of yeasts often differ in vitamin contents (see Introduction). Wagner (1944, 1949) showed that the nutritional requirements of *D. aldrichi* are not satisfied by certain microorganisms on which the related *D. mulleri* develops successfully. Da Cunha, Dobzhansky, and Sokoloff (1951) found that *D. pseudoobscura* and the related species of *D. persimilis* and *D. azteca* are attracted in their natural habitats to various species of yeasts exposed as baits. Nevertheless, each species of fly has a pattern of food preferences different from other species.

It is evident that all the microorganisms used in our experiments are acceptable as food for the three chromosomal types of *D. pseudoobscura*, namely ST/ST, ST/CH, and CH/CH (at least, they are certainly sufficient in combination with other microorganisms which doubtless were present as admixtures in the food in our population cages). But it is also evident that some of the microorganisms are relatively more favorable to the heterozygotes, ST/CH, while others favor more the homozygous type, ST/ST. Dobzhansky (1947, 1949, and other papers) has shown that the incidence of the chromosomal types in the population of certain localities undergo changes from month to month and from year to year. Shihata (unpublished) has obtained data which suggest, although they do not prove, that the relative frequencies of the different species of yeasts in the environment of the flies also undergo seasonal changes. It is tempting to suppose that the genetic changes in the composition of the fly populations are caused, at least in part, by the changes in their nutritional regimes, which in turn are due to variations in the microflora of their habitats.

However, that may be, it is evident that the relative adaptive values of the chromosomal types in *D. pseudoobscura* are extremely sensitive to changes in their environments. A polymorphic species, which contains a variety of such types in its populations, is adaptively more versatile than a more uniform species, and better able than the latter to occupy and exploit a diversity of habitats.

Summary

Experimental populations of *Drosophila pseudoobscura* were kept in population cages and supplied with food containing different species of yeasts or bacteria. The Drosophila populations were mixtures of individuals with Standard or with Chiricahua gene arrangements in their third chromosomes. The microorganisms which served as food were isolated from the intestinal canals of *Droso-*

phila pseudoobscura in the same regions in which the ancestors of the flies used have been collected.

The relative adaptive values of the Standard homozygotes, Standard/Chiricahua heterozygotes, and Chiricahua homozygotes vary depending upon the microorganism used in the food of the flies and their larvae. In some populations the heterozygotes showed heterosis, i.e., were superior to both homozygotes; in other populations the heterozygotes were inferior to Standard homozygotes. These results show that the genes carried in chromosomes with different gene arrangements make their carriers adapted to different foods. It is suggested that nutritional factors may be very important in the distribution and in the relative frequencies of the different gene arrangements in the natural populations of *Drosophila pseudoobscura.*

Acknowledgments

This work has been carried out while the writer held a fellowship provided by the Rockefeller Foundation. The writer is deeply indebted to Professor Theodosius Dobzhansky in whose laboratory most of the work has been done, to Professors E. M. Mrak, H. Phaff, and A. El Tabey Shihata for their instruction in microbiology, and to Mrs. Lygia da Cunha for her constant and manifold help. Mr. and Mrs. B. Spassky, O. A. Pavlovsky, and Dr. L. Schneider, and other colleagues at the Department of Zoology of Columbia University have extended to the writer many helpful suggestions and many courtesies.

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THE NATURAL HYBRID BETWEEN COULTER AND JEFFREY PINES

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INTRODUCTION

During recent years, biologists have developed an increasing interest in hybrids among trees. This interest has been shared equally by the practical forester and by those biologists interested mainly in the genetics involved and in the evolutionary significance that might be attached to these hybrids. In order to study satisfactorily tree hybrids from both points of view, the extent and type of hybridization that has taken place under natural conditions must be determined.

The objective of the present investigation was to determine this for two species of hard pines, *Pinus coulteri* Lamb. and *Pinus jeffreyi* Grev. and Balf., which were considered to be distantly related on the basis of morphological characters. Previous to this study, these two pine species, whose ranges overlap only in central and southern California, were known to hybridize naturally, one hybrid tree having been found in the San Bernardino Mountains (this tree died recently) and several having been located in the mountains of southern San Benito County. In addition, a number of artificial first generation crosses and back-crosses have been produced at the Institute of Forest Genetics at Placerville, California.

In order to study this particular natural hybrid, three independent studies were made: one of the Coulter pine parent in all parts of its range, one of the Jeffrey pine parent throughout its range, and the other of the hybrid wherever it was found. Although the primary interest was in the actual problem of the hybridization and how it was taking place, it was also necessary to study the parental populations, since individual trees of the same species, as well as whole populations within a species, may vary. Therefore, it was essential to determine if one was dealing with the results of hybridization, or merely with inherent variation of the parental species.

EXPERIMENTAL PROCEDURES

In most studies of natural hybridization, large random samples of the population are taken. However, hybridization between Coulter and Jeffrey pines is so infrequent that, if random methods had been used, so few hybrids would have been located that this investigation would have been meaningless. Furthermore, the criteria used were so detailed that a thorough study was necessary for each tree, not merely the taking of a leaf or cone as is so often done in mass collections. Therefore, an attempt was made to locate all possible hybrids; after one was located it was sampled as were several nearby trees of both parental species. This sampling technique precludes the use of the usual statistical methods of analysis but results in a more intensive study of the hybrids.

In order to determine the extent of variation of the parental species, samples of populations were taken in all parts of their ranges. Coulter pine populations were sampled from nine different geographical regions, ranging from Contra Costa County in the north to southern San Diego County. Ten populations of Jeffrey pine were sampled, this species having a greater latitudinal distribution than Coulter pine, with samples being obtained from Humboldt and Lassen Counties in the north to southern San Diego County. Hybrids were sought in several areas where the two species grow intermixed, and, in this

TABLE 1. *Criteria and index values used for hybrid determination*

Criteria	Index value			
	Typical Coulter		Typical Jeffrey	
Cone	12		0	
Specific gravity		5		0
Length		3		0
General appearance		4		0
Seed	5		0	
Ratio, wing to seed length		2		0
Seed coat thickness		3		0
Foliage	12		0	
Bud-general		4		0
No. lines of stomata		1		0
Stomata cross-section		2		0
Endodermal walls		2		0
Stomata wax shape		2		0
Needle flexibility		1		0
Oleoresins	11		0	
Total	40		0	

investigation, they were located in five separate regions in central and southern California.

There were many criteria that might have been used to differentiate between Coulter and Jeffrey pines; the difficulty experienced here was not so much in finding differences between these two species as it was in determining which of the numerous differences were most important in the interpretation of results. Characters were judged on the basis of their importance and their uniformity within species as well as their differences between species since such characters best allow the degree of hybridity to be determined. Twelve major character differences between the parental species were chosen (see table 1); these were morphological, anatomical and biochemical in nature with the gross morphology of cones and needles, the anatomy of the needles, and the biochemical relationships shown by the oleoresins being studied.

THE PARENTAL SPECIES

Both parental species were analyzed using the characters listed in Table 1 to determine how much variation is present within each of them, either between separate populations or between individuals of the same population. Both species were remarkably uniform in most characters; only in those characters more or less directly correlated with site, such as cone size, were any significant differences found. In neither parental species was evidence of distinct geographic races found, based on the characters studied (See Figure 1).

Despite this apparent uniformity, Coulter pine is found with a variety of plant communities which occupy very different

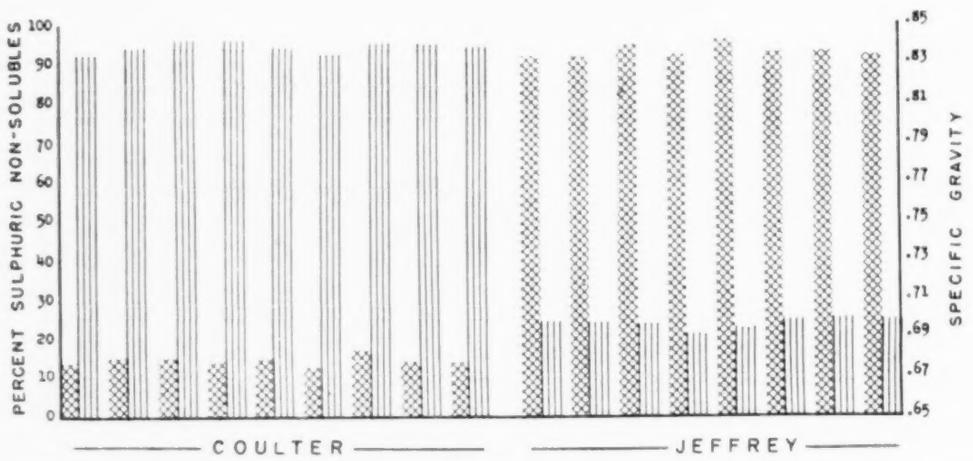

FIG. 1. Constancy of two oleoresin characters shown by samples from populations from all parts of the species range. The cross-hatched area represents sulphuric acid non-solubles, while the area of vertical lines represents specific gravities of the volatile oils.

sites. The common situation is to find it growing on the hot, dry ridges along with chaparral and various kinds of oaks but with no other conifers. However, on several of the higher peaks of the Coast Ranges, it was not restricted to such areas. A good example of this is found in the Santa Lucia Mountains (Monterey County) where Coulter pine was growing not only in chaparral but, in addition, was found at various locations with Jeffrey pine, ponderosa pine (*Pinus ponderosa* Dougl.), Santa Lucia fir (*Abies venusta* K. Koch), sugar pine (*Pinus lambertiana* Dougl.), coast redwood (*Sequoia sempervirens* Endl.) and numerous species of oaks. In some areas it was even growing on the moist north-facing slopes, competing mainly with the very shade tolerant tanoak (*Lithocarpus densiflora* Rehd.). Regardless of the ecological situation in which it was found, the characters investigated were remarkably uniform throughout the range of Coulter pine.

In a few cases, striking differences were observed in the phenotypic appearance of the trees, even though they were very much alike in the 12 characters studied. In some regions there were small areas where the Coulter pines were tall, straight and small limbed, as opposed to the usual large limbed, scrubby type. Often these were associated with site differences and appeared to be a response of similar genotypes to different habitats. In other cases, however, where site conditions appeared to be uniform, the two types were found growing together; all such cases occurred in regions where hybridization had taken place and it appeared they were the result of past introgression of the genes, which control the Jeffrey pine growth form, into Coulter pine. However, this supposition cannot be proved unless suitable genetic tests are made.

Where the two species were growing together, Jeffrey pine appeared to be more restricted than Coulter pine in the sites it would occupy; however, Jeffrey pine has much the greater latitudinal range of the two, and is found at the higher elevations. Both species may be found growing on serpentine soils, but in the northern part of its range, Jeffrey pine is outstanding among pines in its ability to tolerate serpentine conditions. Some biologists felt that Jeffrey pine growing on serpentine soil would differ from that growing on non-serpentine areas. Therefore, populations on each soil type were sampled in Plumas County, but, based on the 12 characters analyzed, no significant differences could be found between the two, making it appear that there is not a definite serpentine ecotype based on these measurable phenomena; however, further study might show a physiological difference between the two sets of populations.

The slight differences among the populations of both species can best be illustrated by the oleoresin characters, as shown in figure 1. Since the populations represented by these graphs are plotted from north to south (left to right) any latitudinal variation should be immediately visible. The uniformity of the per cent of sulphuric acid non-solubles and the volatile oil specific gravities for all populations of both species is remarkable; the contrast in magnitudes of the values for Jeffrey and Coulter pines is also outstanding.

It must be emphasized that since the object of this problem was not primarily that of studying the parental populations, the numbers of populations and size of samples within these populations were restricted. Also, the 12 characters analyzed were chosen for their uniformity within each species and for their obvious differences between the two species, since it is only by using such characters that the degree of hybridity is best determined. If other characters had been chosen to show the maximum variation, possibly some geographic races could have been recognized.

The Hybrids and Hybrid Derivatives

A hybrid between *P. coulteri* and *P. jeffreyi* would seem to be unexpected be-

cause of the very distinct differences between them. These two species of hard pines are distantly related, according to their botanical classification. Shaw (1914) classes Jeffrey pine among the group Australes (this includes the western and southern yellow pines) while he lists Coulter pine as being a member of the group Macrocarpae (including digger and Torrey pines). Judged on the basis of morphological, anatomical and biochemical characters, they are separated more definitely than most species of hard pines within their respective groups.

Nevertheless, hybridization does take place naturally and artificially. Naturally it occurs so infrequently in the region where the two species grow intermixed that a large number of trees must be examined in order to locate a very few hybrids. It was anticipated that during the field collections, one or several areas might be found where hybridization was an apparent common occurrence, but no such area was located. However, whenever one hybrid was found, at least one or a small group of hybrid derivatives were also found in the same locality.

Up to the present time the word hybrid has been used in a general sense with no clear-cut definition as to its meaning. Some persons feel that only the results of the first cross, or F_1, should be called a hybrid, and the backcrosses and segregates should be called hybrid derivatives; others feel that the crossing of any two unlike individuals results in a hybrid. This latter idea will be used in this paper, since a study of the natural hybrid can not show absolutely whether one is dealing with a first cross even though the tree may have characters intermediate between the two species. Likewise the term backcross will be applied to those hybrids containing a preponderance of characters of one parental species, such as would be obtained in a backcross, even though they could conceivably be segregants from the crossing of two hybrids. This is a rather remote possibility, however, since so few hybrids are found growing in any area. If

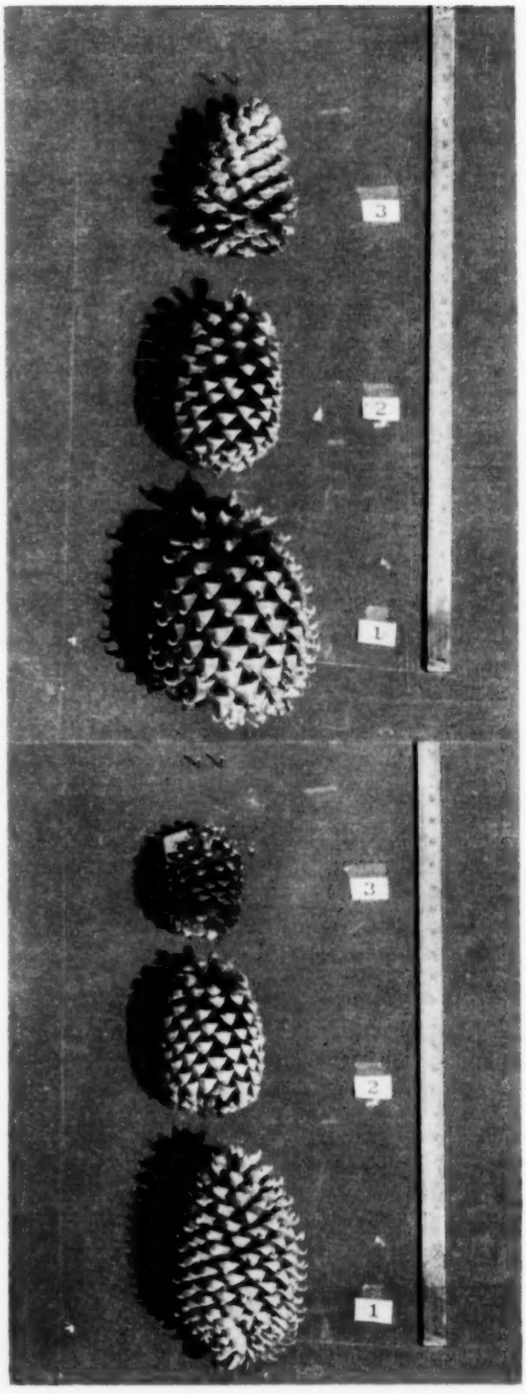

FIG. 2. Cones from the parent species and hybrid from Riverside County and from San Diego County (bottom), showing the intermediacy in characters of the hybrid. Note especially the ends of the cone scales. (1) Coulter pine, (2) Hybrid, (3) Jeffrey pine.

segregation does occur, it would then appear that under natural conditions those segregates favoring the Jeffrey pine parent usually do not become established. Of the 40 Coulter-Jeffrey hybrids analyzed in this study, only four trees from one small canyon in San Benito County showed a preponderance of Jeffrey pine characters; all the others were intermediate or definitely more similar to Coulter pine.

While making the field collections, trees were tentatively identified as hybrids mainly on the basis of cone characters. The intermediacy of the cones from hybrid trees is illustrated by figure 2. This tentative identification was then checked in the laboratory and the trees definitely classified, judged on the 12 characters listed in table 1. In order to correlate the different characters, use was made of the hybrid index, proposed by Anderson (1936) and very concisely summarized by Stebbins (1950, pp. 265); the index values used are listed in table 1.

The total index value assigned for all 12 characters was 40 for Coulter pine and zero for Jeffrey pine. In some cases there were trees for which all 12 characters could not be scored. This was often true of seed characters. When this occurred the tree was graded only on the basis of the characters present, then adjusted to a basis of 40 possible points. Each tree sampled was then given an index value; it was found that Coulter pine from a "pure" area (no Jeffrey pine present) had index values ranging from 37 to 40 points and that Jeffrey pine from a "pure" area had index values ranging from 0 to 4 points. Therefore, any tree possessing less than 37 or more than 4 points was considered to be a hybrid or hybrid derivative.

The use of the oleoresin character in the index deserves special mention here. Four characteristics of the volatile portion of the oleoresin were measured; these were the specific gravity, the index of refraction, the per cent of sulphuric nonsolubles and the optical rotation, three of

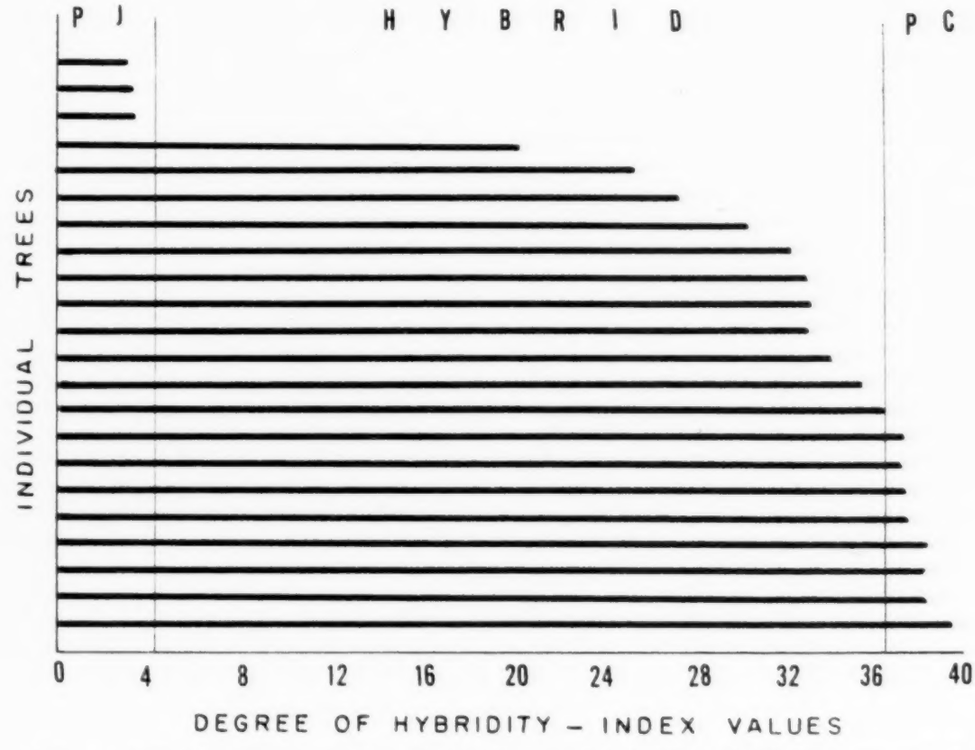

FIG. 3. Graphical representation of the degree of hybridity of all the trees sampled in the Benton's Ranch Area (southern San Diego County). Degree of hybridity was determined by the use of Anderson's hybrid index and was based on 12 characters.

which were used by Mirov (1946). All of these were definitely measurable criteria requiring no personal judgment. However, preliminary examination indicates that these characters, especially the first three mentioned, are very closely correlated and a measure of any one of them would be sufficient; here, all four were used and their combined results recorded as the oleoresin character. It appears they are controlled by the same set of genes, although this number has not been determined. Because their characteristics could be measured quantitatively with great exactness, the writer feels that the oleoresins should carry a weight similar to the foliage or cones so they were assigned the index value of 11 points.

Graphs were constructed for the five areas where hybrids were found. Four of them had an appearance simliar to that for Benton's Ranch (San Diego County), illustrated by figure 3. Note that all hybrids were either intermediate in nature or had index values indicating they were backcrosses to the Coulter pine parent. This was the common condition, and either no backcrosses to the Jeffrey pine parent were formed, or, if they were, they could not compete and were soon lost from the population. In addition, it was observed that hybrids were found only in those regions where there was an excess of Coulter pines over Jeffrey pines, and no hybrids were found where there was a preponderance of Jeffrey pines. According

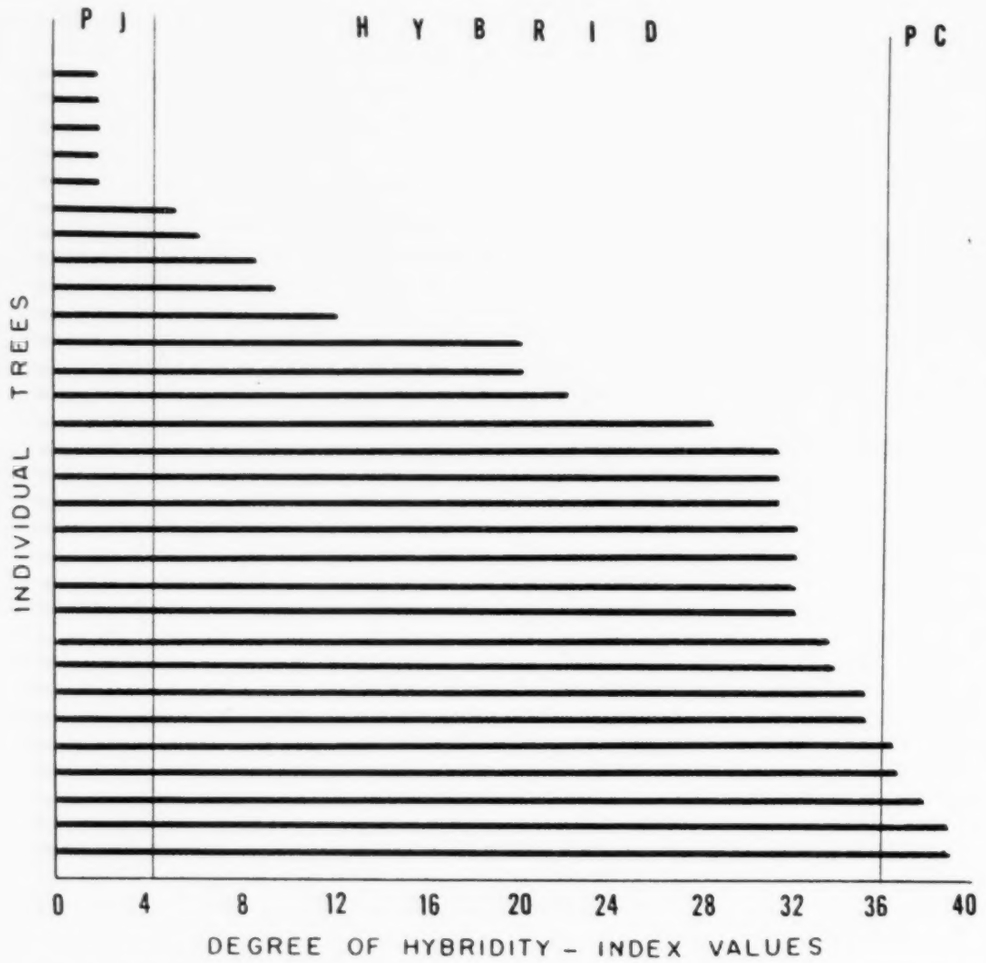

FIG. 4. Graphical representation of the degree of hybridity of all the trees sampled in the Idria Area (southern San Benito County). Degree of hybridity was determined by the use of Anderson's hybrid index and was based on 12 characters.

to Mr. Righter, of the Institute of Forest Genetics, in many regions the staminate catkins of Coulter pine mature before those of Jeffrey pine. This results in Coulter pine pollen being released when the Jeffrey pine female conelet is receptive, so the conelet may be pollinated before the Jeffrey pine pollen is shed. The fifth area, represented by figure 4, located in southern San Benito County near Idria, contained intermediates and backcrosses to the Coulter pine parent, but, in addition, included several trees with characters favoring the Jeffrey pine parent, indicating that introgression is proceeding in both directions. The cones from trees of various degrees of hybridity growing at Idria are illustrated by Figure 5.

It was previously stated that hybrid trees were very hard to find where the two species are growing intermixed. The same phenomenon is observed for these pines as Stebbins (1950, pp. 63) found in the oaks, that hybridization may occur at one location while only a short distance away, under what appears to be identical conditions, no sign of hybridization can be found. However, it seems significant that at least some hybridization is found in all five general geographic regions studied where the ranges of the two species overlap, regardless of the site conditions or latitudinal distribution.

Most hybrids were found growing under severe site conditions, such as on rocky outcrops or on cliffs, or were being crowded out by the parental populations. This suggests the lack of a suitable habitat for their establishment (Anderson, 1948), resulting in their inability to compete with the parental species. In the majority of regions studied the habitat was relatively undisturbed, except at Benton's Ranch (where the hybrids were growing around the corrals at a meadow's edge) and at Idria (where the area had been logged for mine props). It was in these two areas that hybridization was the most common.

Since hybridization between these species appears to be so infrequent, the question arises as to its long-range effect, or evolutionary significance. In the writer's opinion, the evolutionary importance of these hybrids has been relatively slight. In most cases, a distance of only a few hundred yards is all that shows any trace of the results of hybridization; the visible results of backcrossing and segregation seem to be centered in the small area where the first hybridization took place. The lack of long-range effects is further emphasized by the constant character of the parental populations, with their similarity in "pure" and hybridizing areas.

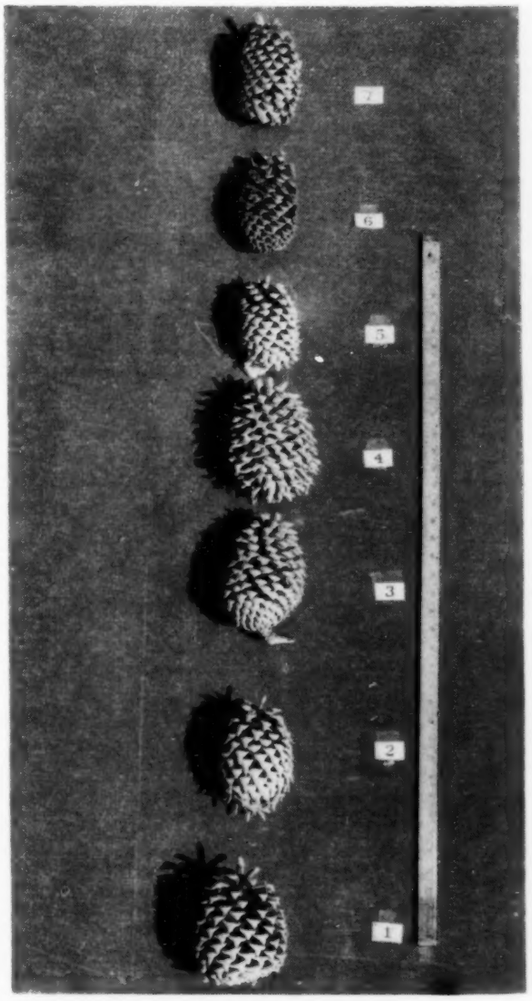

FIG. 5. Cones from seven hybrid trees from San Benito County. Numbers 1 and 3 are intermediates (F_1?), numbers 6 and 7 are backcrosses to the Jeffrey parent (or segregates) and the others are backcrosses to the Coulter parent (or segregates).

However, these hybrids may become increasingly important as a result of changes brought about by man's activities (Anderson, 1949). This appears to be the situation in the region near Idria where logging and fires have greatly altered the habitat.

Introgression, then, does take place (usually Jeffrey characters into Coulter pines), but the evidence from this study shows that its extent is limited. This seems to indicate that, if conditions in the future remain the same as they were in the past, *P. coulteri* and *P. jeffreyi* will remain as distinct species, and no great amount of merging will take place. This statement of opinion must be restricted only to the particular areas studied and the particular criteria used for this problem.

A great deal of speculation has taken place on the relationships among species of pines. As stated earlier, Shaw (1914) lists Jeffrey pine as a member of the group Australes and Coulter pine as a member of the group Macrocarpae, and classifies these two groups as being not closely related. Therefore, the Coulter-Jeffrey pine hybrid is an inter-group cross, a type not as common as the intra-group cross. In discussing this problem, it must be recognized that Coulter and Jeffrey pines may not be typical representatives of their groups. In the past, the idea has been expressed that Jeffrey pine is a linking form between the two groups; the same role has been suggested for Coulter pine. Since hybridization and gene exchange between Coulter and Jeffrey pines have now been found to take place naturally in several different regions, some biologists feel that the two groups, Australes and Macrocarpae, are genetically closely related. The writer feels that they may be more closely related than indicated by Shaw (1914), but that the localization of the effects of introgression and the morphological differences point to their identity as distinct groups. Righter and Duffield (1951) have prepared a summary of the results of the crossing program carried on at the Institute of Forest Genetics. As this crossing program progresses, and as existing natural hybrids are studied, the relationship patterns among the pines will become clarified.

Summary

A study of the natural hybrid between Coulter and Jeffrey pines was undertaken to determine the extent and importance of hybridization that has taken place between these two species. The hybrids and parents were analyzed using 12 of the more important characters, including the oleoresins. Investigation of a limited number of samples throughout the range of the parent species indicated that both Coulter and Jeffrey pine are relatively constant species, with little evidence of distinct local races.

The occurrence of natural hybridization between these two pines is uncommon. In no area do the hybrids or hybrid derivatives approach either parent in numbers; on the contrary, usually an extensive search of many trees was necessary to find a single hybrid. In some localities where the two species grow together, there is no evidence of hybridization, while nearby areas show a considerable amount of it. However, it seems significant that some hybrids were found in all five geographic regions studies where the two species occur in association. Hybrids usually were found in areas where Coulter pines greatly outnumber Jeffrey pines.

Enough hybrids and hybrid derivatives were found to state definitely that introgression does take place. The use of Anderson's hybrid index disclosed that in one area, introgression was proceeding into both parental species. In all other areas, introgression appears to be proceeding only into the Coulter pine populations, and all intergrades are found, from the intermediate to typical Coulter pine. Because of the rarity and localization of hybrids, it is concluded that hybridization and consequent introgression has been of

little evolutionary significance, although man's activities may produce a more suitable habitat for the hybrids in the future. Since gene exchange does take place naturally, some biologists feel Jeffrey and Coulter pines are genetically closely related species; however, only further results from the crossing program and further study of natural hybrids can clarify the relationship pattern.

The author is indebted to the members of the Institute of Forest Genetics who made available valuable materials and who helpfully advised in the preparation of the manuscript. The use of laboratory space and equipment made available by the faculty of the School of Forestry is much appreciated. The guidance in the preparation of the final manuscript by Dr. G. L. Stebbins of the Genetics Division of the University of California was very valuable.

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NOTES AND COMMENTS

CORRECTIONS

S. C. Reed

Mr. Alan Robertson of the Institute of Animal Genetics, University of Edinburgh, has very kindly pointed out an error in a paper by S. C. Reed and E. W. Reed, entitled "Natural selection in laboratory populations of *Drosophila*," published in Evolution, 1948, vol. 2, 176–186. The section concerned is that called "Effect of Natural Selection" on p. 184.

It was stated there that the selection value (W) is 0.286 for $\frac{wmf}{wmf}$ females as compared with 1 for $\frac{wmf}{M5}$ females. The above statement is correct but the subsequent statement that one should take the square root of this value, or the cube root, to correct for the number of generations ensuing between counts of the flies, is both unnecessary and incorrect. It is not necessary to adjust for the generations between observations of the flies as the population is in equilibrium from generation to generation and the length of time between counts is irrelevant.

We are grateful to Mr. Robertson for his acuity. The correction strengthens the major observation considerably. The selective value for homozygous females of 0.286, roughly 0.3, can be accepted without adjustments. The statement, repeated in the summary of the original paper, that the selective value for homozygous females is from 0.5 to 0.7 per generation, is incorrect and it is now obvious that the first value of about 0.3 is the proper one to use. The selective pressure against the homozygous female, and in favor of the heterozygous female, is much stronger than we had previously assumed.

It is opportune to report here a minor correction in the second paper in the series on "Natural selection in laboratory populations of *Drosophila*," in Evolution, 1950, vol. 4, p. 39. In the body of the grid at the extreme top of page 39, the printer omitted the value for the ww zygotes which is 0.162 ww. This omission could be rectified easily by the reader and in no way affects the rest of the paper.

SEX DETERMINATION IN THE HONEYBEE

Ann R. Sanderson and D. W. Hall

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In a recent article (1) titled "Sex chromosome in honey-bee" Warwick Estevam Kerr of São Paulo University made certain statements regarding our published work on bee cytology that may be misleading (2). Possibly owing to language difficulties he conveys the impression that we are not in agreement with earlier workers on the chromosome number in the honey bee. In an article in Nature (2) we stated that we found the same number as Meves and Petrunkewitsch, i.e., 32 in the female and 16 in the male. Our relevant observations may be summarised as follows: in the spermatogonia one chromosome is somewhat larger and hooked and is very striking in late anaphase and in the oogonia appears to be present in duplicate; no reduction occurs in the spermatocyte but in the oocyte reduction to 16 takes place.

In his article, Kerr gives an account of the elimination of what he considers to be an X chromosome in the spermatocytes, but the evidence he puts forward in support is not convincing. The photograph submitted is very indistinct and his "photocopy" is misleading, for chromosomes are not usually extruded from the second spermatocyte as a naked mass but are contained within a nuclear membrane in a small daughter cell. His observations on the heteropycnosis of the so-called X chromosome and its extrusion from the second spermatocyte are presented as further proof of similar conclusions on *Apis mellifica* L. published by another worker, F. J. Manning (3). In no way does Kerr's evidence strengthen Manning's hypothesis of the existence of sex chromosomes. Kerr is prepared to accept Manning's evidence on differential maturation in the egg but in our opinion Manning's evidence is unsatisfactory and far from complete.

Since reading Kerr's article we have re-examined some of our preparations but find no evidence which would warrant support of the theory of sex chromosomes in the honeybee. Admittedly one chromosome is outstanding in size and shape but one should be cautious about

assigning to it any function of sex determination. Although as we have stated elsewhere (4) the existence of sex chromosomes may yet be satisfactorily demonstrated, in our opinion the published evidence to date does not warrant the acceptance of any theory of sex determination in the honeybee other than that of haplodiploidy.

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(1) KERR, W. E., *Evolution,* **5**: 1 (1951).
(2) SANDERSON, A. R., AND HALL, D. W., *Nature,* **162**: 34 (1948).
(3) MANNING, F. J., *The Microscope,* **7**: 7–12 (1949); **8**: 1 (1950).
(4) SANDERSON, A. R., AND HALL, D. W., *Endeavour,* **10**: 37 (1951).

COMMENT ON ECOLOGY AND EVOLUTION

CHARLES H. LOWE, JR.

A brief statement here regarding a commentary on the recent Principles of animal ecology [1] seems pertinent at this time. In a concluding remark on organization of the section of the book on evolution, Pitelka (EVOLUTION, **5**: 84, 1951) states, "as a part of a book on ecology, [it] might have been more unified if it had been consistently guided by some basic theme as the pyramid of numbers and the evolutionary consequences of fundamental differences between the several trophic levels." This suggestion for such orientation about the biotic pyramid comes naturally from an outstanding community ecologist.

Since I have given some attention to this same section, "Ecology and Evolution" written by A. E. Emerson, it appears to me that there is perhaps a still more fundamental "theme" with regard to unification of organization of this subject. As a part of a book on ecology, it might have been more unified if it had been consistently guided by some basic motif such as the opportunistic nature of evolution with adaptation the orienting factor (Simpson, 1949, The meaning of evolution) and the ultimate physiological-genetical nature of adaptation, both internal and external, including social. As for the biotic pyramid, it is an observed *resultant* (at any one point in time and space) of evolutionary process, the over-all trend of which has been an elaboration and diversification of the biota, and, hence concomitantly, an elaboration and diversification of the food chains forming the basis of the ecological concept—the pyramid of numbers (the biotic or Eltonian pyramid). Of course the important significance of the biotic organization labeled by the ecological term cannot be minimized.

It appears that the material presented by Emerson in this section was organized sometime previous to the recent beneficent surge of inquiry into evolutionary mechanism. Rather than viewing his extensive treatment of ecology and evolution as "setting the scene" for a synthesis with its basic theme the biotic pyramid, or some other more purely community concept, perhaps it would be more meaningful if viewed as a departure point for a needed synthesis of ecology and evolution that primarily would be concerned with inquiry into the ultimate physiological-genetical basis of adaptation (seemingly the orienting factor in evolution, that appears to be largely, if not wholly, opportunistic) and the intricate relations of this basis to natural selection. Such a synthesis, by its very fundamental nature (already alluded to by other authors), would embrace at the same time what are apparently the real factors producing the results that form the foundations of many of the concepts and unique interpretations commonly associated with modern as well as classical community ecology.

[1] W. C. Allee, A. E. Emerson, O. Park, T. Park, and K. P. Schmidt. Principles of animal ecology. W. B. Saunders Co., Philadelphia and London, 1949: i–xii, 1–837, figs. 1–263.

ANIMAL EVOLUTION [1]

DEAN AMADON

This textbook contains a comprehensive discussion of all the main aspects of animal evolution (and not merely its causes). The genetic background is thoroughly discussed, as are such topics as macroevolution, orthogenesis, etc., though as regards the latter Carter acknowledges his heavy reliance upon Simpson's "Tempo and Mode." As a textbook "Animal Evolution" is

[1] Animal Evolution. A Study of Recent Views of Its Causes. By G. S. Carter. Sidgwick and Jackson, London (Macmillan, N. Y.), 1951, i–xv; 1–368; figs. 1–63; $4.50.

presumably intended for graduate students or advanced undergraduates. It is too much to expect that a book covering the entirety of such a large and rapidly changing field will please everyone in all respects. There are, as a matter of fact, more doubtful conclusions and statements in the present book than in what are generally regarded as the topflight recent books on evolution, those by Huxley, Simpson, Rensch, Mayr, Dobzhansky, Stebbins, and a few others. Carter, for example, stresses non-adaptive evolution, but all recent work tends to minimize the importance of this. It is unfortunate that he chose as an example the color patterns of the European snail (*Cepaea*) inasmuch as Cain and Sheppard have just shown that these too, at least in their broad effects, are probably adaptive and protective. Again, Carter makes much of the difference between quantitative and qualitative evolutionary change and exhumes, unwisely it would seem, the term *aristogenesis* of Osborn for the latter. As Simpson has somewhere said, almost any qualitative differences can be bridged by quantitative steps, and it is doubtful whether "qualitative" mutations are really such an unknown entity as Carter would have us believe. Perhaps for pedagogic reasons, he seems to enjoy setting up such straw men, but he is sometimes unnecessarily reluctant to knock them down again. His handling of the "morphological" species concept is another example of such treatment. In his treatment of clines Carter is probably in error in stating that stepped clines are more frequent than "internal" (gradual) ones, and I doubt whether the latter present quite such a genetic problem as he implies. There are other minor points that might be mentioned, e.g., the statement that the fish hawk or osprey (*Pandion*) is unspecialized because it is nearly cosmopolitan in range. That the osprey is a highly specialized hawk seems obvious.

"Animal evolution" is a well-planned and, by and large, satisfactory volume but, in the reviewer's opinion, its value as a text could have been enhanced if it had received a thorough going-over by a few competent critics.

EVOLUTION OF THE VERTEBRATES [1]

EDWIN H. COLBERT

For more than thirty years William King Gregory trained graduate students at Columbia University in the field of vertebrate evolution. In this long career as a teacher, he succeeded Professor Henry Fairfield Osborn, who had founded graduate training in vertebrate paleontology at Columbia. Dr. Gregory was not only a great teacher, under whose tutelage many of the outstanding vertebrate paleontologists of America and Europe received their training, but also he was an active research worker in the field of comparative vertebrate anatomy and evolution. With the collections of The American Museum of Natural History at his disposal he carried on studies among all of the vertebrate classes and established himself as a great authority on the backboned animals from fishes through mammals. His knowledge of the vertebrates was and is encyclopedic.

The work now under consideration represents a compendium of all the knowledge of vertebrates that he accumulated during his long years as an active research worker and a teacher. It is a comprehensive survey of the evolution of the vertebrates, including both fossil and recent forms. It is issued in two volumes, the first of 736 pages containing the text and bibliography, the second of 1013 pages being devoted to the illustrations.

The text is divided into six parts, and each of these into several chapters. The six parts deal successively with the invertebrate background of the vertebrates, the emergence and early history of the vertebrates, the transition from aquatic gill-breathing to terrestrial lung-breathing vertebrates, the rise and adaptive radiation of the mammals, the evolution of the primates, and finally a section entitled "Retrospect and Prospect."

Here one will find much of the evidence as shown by fossil and recent forms for the evolution of the vertebrates. Interspersed among the purely descriptive portions of the text are sections dealing with more theoretical aspects of the subject, such as the origin of tetrapod limbs, the origin of the tetrapods themselves, the origin of reptiles and the origin of mammals. Also there are discussions of concepts developed by Dr. Gregory, such as polyisomerism and anisomerism, heritage and habitus characters and the irrevocability of evolution. Since this is frankly an account of vertebrate evolution as revealed through the study of comparative anatomy, one does not find here any consideration of evolutionary studies made along other lines by many recent workers in the field. Thus, there

[1] William King Gregory. 1951. Evolution Emerging. A Survey of Changing Patterns from Primeval Life to Man. The Macmillan Company, New York. Vol. 1 (Text), i–xxvi, 1–736 pp.; Vol. 2 (Figs. and Pls.) i–vii, 1–1013 pp.

is little discussion of the modern approach to evolution based on work in genetics, and virtually no attention given to the many studies that have been made in systematics, the problem of speciation as based on statistical analyses and the like. Such is not Gregory's purpose. His is a survey of the rise and development of vertebrates and of the structures which comprise vertebrate anatomy.

In this light, the work will be of particular value to students of vertebrate evolution, especially comparative anatomists and vertebrate paleontologists. Here one will find a summary of Gregory's work on the vertebrates that, during the past four decades, had so much influence on the subject of vertebrate paleontology. For such students the second volume of the work, devoted entirely to comparative figures, will be of extraordinary value.

There is an extensive bibliography, arranged in parts coinciding with the six large divisions of the text.

INBREEDING AND DISEASE?[1]

DEAN AMADON

The so-called Solitaire, *Pezophaps solitaria*, of Rodriguez Island in the Indian Ocean was a giant, flightless pigeon related to the better-known Dodo of Mauritius. Leguat, one of the few naturalists to record anything of this bird in life, wrote in the year 1708: "The bone of their wings grows greater towards the extremity, and forms a little round mass under the feathers as big as a musket ball. That and its beak are the chief defenses of this bird." The bones of *Pezophaps*, of which an abundant supply have been dug from swamps, are known to show numerous ill-healed fractures, hitherto assumed to be the result of blows from the "armored" wings. In the present paper Ottow gives the results of a study of a sample of this material borrowed from the British Museum. He found that "a macroscopical and X-ray examination revealed a characteristic bone disease, which appears in two forms. . . . The latter form can lead to bone fractures . . . it is probable that we have in *Pezophaps* a bone disease . . . which should be interpreted as a hereditary disease of the mesenchyme tissues . . . originating from a mutation of pathological value which could spread due to narrow geographical isolation, inbreeding and lack of selection. The case of *Pezophaps* can be compared to a breeding experiment with harmful genes carried out in Nature . . . here for the first time the existence of a well defined hereditary disease—that is not only [merely] an overspecialisation of harmful nature—has been demonstrated to occur in Nature." This interesting possibility— that a harmful genetical condition has become widely established in a small population through random gene fluctuations of the type postulated by the "Sewall Wright effect"—cannot, unfortunately, be considered as fully established. Ottow himself states that the material sent to him was "selected."

There is, of course, little basis for an estimate of the original population of *Pezophaps*. Rodriguez is said to be about sixteen kilometers long; this indicates an area of about 500 acres. It is hardly likely that the total population of this goose-sized, terrestrial bird exceeded 500 or 1000 pairs and it may have been much less. This would seem to be a small enough population for deleterious genes to have become established during the tens or hundreds of thousands of years required for the evolution of this endemic, monotypic genus on Rodriguez.

[1] Ottow, B. 1950. Die erbbedingte Osteogenesis dysplasticoexostotica der ausgerotteten flugunfähigen Riesentaube *Pezophaps solitaria* der Mascareneninsel Rodriguez (with English summary). Kungl. Svenska Vetenskapsakademiens Handlingar. Fjärde Ser., **1** (9): 1–37, 8 pls.

THE GEOBOTANICAL SIGNIFICANCE OF POLYPLOIDY[1]

THOMAS W. WHITAKER

As stated by the authors, the paper under review is the first of a series of studies on the geobotanical significance of polyploidy. It consists mainly of a critical review of the entire subject of polyploidy and latitude, intercalated with some original observations and experimental work of the authors. The evidence submitted, demonstrates that at least for the flora of Europe, the frequency of polyploidy increases with an increase in latitude. There are certain ex-

[1] Löve, A. and Löve, D. 1949. The geobotanical significance of polyploidy. I. Polyploidy and latitude. Port. Acta Bio. Series A—R. B. Goldschmidt Vol.: 273–352.

ceptions; but for the most part, the above statement seems to be a sound generalization. However, there is no reason to believe that this rule would necessarily hold true in other areas, where the floras have not come under the direct influence of Pleistocene glaciation, as has the flora of Northern Europe.

Having established the fact that polyploidy increases with latitude, the next question is to produce a practicable explanation of the phenomena. The authors have approached this problem by examining in great detail the comparative physiology and morphology of diploids and polyploids.

It is concluded that the formation of new polyploids is completely at random, but they are more variable than their diploid relatives, and thus are adapted to a wider range of conditions. As a result, polyploids in arctic and boreal regions will survive and disperse from areas where edaphic and climatic barriers restrict or immobilize the dispersal of diploids. The increased ability of polyploids to form new ecotypes, combined with superior means of dispersal, is apparently due to their genetic as well as physiologic adaptability to extreme environmental conditions acquired through an increase in the total number of genes.

The authors have evaluated, and brought some order and meaning to the scattered and isolated literature of this important subject. Their Bibliography of almost 350 titles will be very helpful to students whose research interests may touch upon this field. It is worthwhile to note that our knowledge of polyploidy in floras other than Europe is extremely piecemeal, or even nonexistent. This is particularly true of the tropical floras of both hemispheres. Thus, the present contribution must be commended for laying the foundation for attack upon the larger and much more difficult problems that are sure to be found in other floras.

COMMENTS ON EVOLUTIONARY LITERATURE

By Ernst Mayr

Pair formation.[1] An important study on sex recognition and pair formation in a bunting. Both male and female of the yellow hammer can identify the sex of previously unknown individuals by optical, acoustic, and behavior clues. Any of the three kinds of clues alone is sufficient. There is a definite pair formation ceremony which, however, is performed many times by various partners until the final pair is formed. This is followed by an "engagement period" of about six weeks until the first copulations take place. It is evident what a powerful mechanism pair formation is to prevent hybridization with alien species.

Biological species differences.[2] The two very closely related and partly sympatric species of European flycatchers, *Muscicapa hypoleuca* and *albicollis* hybridize occasionally. The authors give a complete comparative repertoire of the vocal expressions of the two species. Fifteen songs or calls with specific biological significance are known. Ten of these are very similar or identical in both species. Only song and warn note are quite different. One call seems to be limited to *hypoleuca*, one to *albicollis*, without equivalent in the other species. This vocal repertoire confirms the very close relationship of the two species.

Species hybrids.[3] Perhaps the best known and most frequent hybrids between good species of North American birds are those between the Blue-winged and Golden-winged Warbler. No breeding work has been done, but the author's analysis of abundant museum material indicates that the chief color differences are due to three major genes. The various possible combinations are recovered in nature approximately in the expected frequencies.

Competition between Drosophila species.[4] Gause's rule that no two species can coexist in precisely the same niche is also true for *D. melanogaster* and *D. funebris* when both occur in the same culture bottles. In fresh food *melanogaster* is superior, in old food *funebris*. Presumably the two species utilize different microorganisms.

River barriers.[5] The role of Grand Canyon (middle Colorado River) in speciation and zoogeography has been studied by Grinnell and other writers. The present study deals with the

[1] G. Diesselhorst. 1951. Erkennen des Geschlechts und Paarbildung bei der Goldammer (*Emberiza c. citrinella* L.). Ornith. Ber., **3**: 69–112.

[2] L. von Haartman and H. Löhrl. 1950. Lautäusserungen des Trauer- und Halsbandfliegenschnäppers. Ornis Fennica, **27**: 85–97.

[3] K. C. Parkes. 1951. The genetics of the Golden-winged × Blue-winged Warbler complex. Wilson Bull., **63**: 5–15 (with color plate).

[4] D. J. Merrell. 1951. Interspecific competition between *Drosophila funebris* and *D. melanogaster*. Amer. Nat., **85**: 159–169.

[5] K. R. Kelson. 1951. Speciation in rodents of the Colorado River drainage. Univ. Utah Biol. Series, vol. XI, no. 3, 125 pp., 10 maps.

upper Colorado River in Utah. It is shown, as might be expected, that it becomes a less and less efficient barrier toward its source. In the southernmost part of the study area twelve species of rodents, but only four subspecies, are common to both sides of the river. Two species and twenty subspecies are confined to the west side, eleven species and ten subspecies to the east side.

Selective polymorphism.[6] A third laboratory joins in the work on the evolutionary significance of the polymorphism in the banded snails (*Cepaea*) of Europe. Schnetter, in a preliminary note, reports on an eight-year study of marked populations. The yellow phenotype prevails in dry, sunny locations, the reddish one in wet woods. The frequency of the yellow unbanded snails in a mixed colony increased 16.2 per cent during a series of dry years. A study of marked individuals indicates differences in habitat selection between different genotypes of the same population. Reproductive and mortality rates are calculated.

Habitat selection by genotypes.[7] Aquatic isopods (*Asellus aquaticus*) showed preference for different light intensities correlated with their pigmentation. The less pigmented the more photophobic. This indicates that cave populations may be started through habitat selection of individuals with incipient cave characters.

Selection for coadaptation.[8] When artificial populations were made from a mixture of Californian and Mexican races of *Drosophila pseudoobscura* there was at first no heterosis among carriers of one Californian and one Mexican third chromosome. After about sixteen generations in a population cage such heterozygotes were clearly superior to either homozygotes. This shows that among the many genetic variants of the original Mexican and Californian strains those were selected which gave the most viable combinations with each other.

Incidental genetic difference.[9] Several lines of poultry that were kept in the same environment showed different resistance to a respiratory disease to which they had not been exposed for at least seventeen years. The genetic basis for the resistance had thus been acquired as a by-product of the genetic divergence rather than as a result of directed selection. Many properties of natural populations, such as incipient reproductive isolation, appear to be acquired often in an equivalent manner.

Natural selection through insecticides.[10] The development of insecticide resistant strains of insects is of the highest interest to the evolutionist as illustrating the action of natural selection. The Bureau of Entomology has published two most useful critical reviews of the literature of this field. Some species have a low ability to develop resistance (e.g., some scale insects), others a very high one. There are laboratory strains of the house fly that are more or less resistant to every insect poison to which they have been exposed. Acquisition of resistance to one poison often conveys also tolerance or resistance to other chemically quite unrelated poisons. In this the insects differ from anti-biotic resistant bacteria. Various unpredictable mutation and selection pressures determine whether or not resistance will be lowered or lost during long periods of non-application of the poisons. Every resistant laboratory strain behaves somewhat differently from every other strain, which is what one expects in view of the complex genetics of the material.

Selection for body size.[11] During the exceedingly severe winter of 1946–1947 most individuals of the mole (*Talpa europaea*) population of the study area were killed off. Small individuals had the best chance to survive. Normal population densities were re-established within three years, but the larger size classes had not yet been filled up. Further studies must show to what extent this is due to slow growth and to what extent to an elimination of the genes controlling large size. Mean size in mountains and in the colder parts of Russia is lower than in western Europe. In the milder western Europe selection normally favors the large-sized, individuals. There seems thus a dynamic balance between the two opposing selective trends.

The effect of ecological mutations.[12] Author calculates that an allele which broadens the ecological tolerance of its carrier may be added to

[6] M. Schnetter. 1951. Veränderungen der genetischen Konstitution in natürlichen Populationen der polymorphen Bänderschnecken. Verh. Deutsch. Zoolog. Marburg, **1950**: 192–206.

[7] W. Janzer. 1950. Versuche zur Entstehung der Höhlentiermerkmale. Naturw., **37**: 286.

[8] Th. Dobzhansky and H. Levene. 1951. Development of heterosis through natural selection in experimental populations of *Drosophila pseudoobscura*. Amer. Nat., **85**: 247–264.

[9] I. M. Lerner, L. W. Taylor, and J. R. Beach. 1950. Evidence for genetic variation in resistance to a respiratory infection in chickens. Poultry Sci., **29**: 862–869.

[10] F. H. Babers. 1949. Development of insect resistance to insecticides I. Bureau Ent. and Plant Quarantine, E 776 (111 titles); II. 1951, E 818 (171 titles).

[11] G. H. W. Stein. 1951. Populationsanalytische Untersuchungen am europäischen Maulwurf. II. Über zeitliche Grössenschwankungen. Zool. Jahrb. (Syst.), **79**: 567–590.

[12] W. Ludwig. 1950. Zur Theorie der Konkurrenz. Die Annidation (Einnischung) als fünfter Evolutionsfaktor. Neue Erg. und Prob. Zool. (Klatt Festschr.): 516–537.

the population without being necessarily superior to the existing alleles. It adds to the utilization of the environment by the species. Such a mutant may actually be inferior to its alleles in all other viability factors. The question is of considerable importance in view of ecological relations of the genetic elements within a balanced polymorphic population. If selection concentrates on the heterozygotes, how do they and the homozygotes divide the various sub-niches among themselves? Neither the ecological nor the mathematical analysis of this complex problem has yet been effected.

Origin of the species flocks in Lake Victoria.[13] About sixty species of the cichlid fish genus *Haplochromis* occur in Lake Victoria. Author divides them into a primitive group of twenty-four species, a more advanced predaceous group of middle depths (seventeen species), and a most advanced predaceous group which is surface feeding (eighteen species). Geological and taxonomic considerations favor the hypothesis that group 1 originated in Pliocene, group 2 in the early and group 3 in the middle Pleistocene. Lake Victoria fluctuated between great extension (being even connected with L. Edward and L. Albert) and partial drying out when it was reduced to a smaller central body flanked by swampy pools and rivers (middle Pleistocene), or more or less disconnected swamps (Pliocene). This favored periods of speciation. The filling of the lake by several Kenya rivers may have contributed species. Speciation in Lake Victoria is thus ascribed by the author to precisely the same two mechanisms postulated by me (**1942**: 215). The date of the first period of speciation (Pliocene) is shown by Greenwood to be much earlier than thought by previous authors.

Ecology and speciation in jays.[14] A very thorough study of the individual and geographical variation of three polytypic species of jays. The species are biologically defined and there are at least two cases where subspecies groups come into contact without full interbreeding. If absence of complete intergradation were taken as species criterion, one would have to recognize thirteen species instead of three. Racial differences in color and proportions can be correlated rather well with features of the physical and floristic environment. Degree of isolation determines amount of difference between adjacent races.

The origin of the subspecies groups in *A. caerulescens* is pushed back to the early Pliocene, on the basis of a "suggestion" made by Epling in 1944 against which some weighty objections have been raised by several authors (see Deevey, **1949**: 1403). Although it is possible that the species of *Aphelocoma* date back to the Miocene, their great similarity makes a more recent origin probable. Two of them are yet virtually allopatric. The method of dating the origin of species by dating the origin of the vegetation form with which they are now associated is full of dangers. The many known cases of strong geographical variation in habitat preference invalidate the organismic concept of the "biome." The habitat is a substrate for an animal, and a species can evolve away from it. Furthermore, dispersal must never be neglected in reconstructions of former histories. The history of island faunas proves abundantly that no continuity of habitats is required to explain the occurrence of the same (or closely related) highland forms on both sides of the isthmus of Tehuantepec. It is doubtful whether former distributions and dates of origin can ever be determined satisfactorily without fossil evidence.

A complicated borderline case.[15] A complicated situation prevails among two closely related groups of Californian garter snakes. An aquatic group consists mainly of the five subspecies, *hydrophilus, aquaticus, atratus, gigas,* and *couchii,* which are strictly allopatric and intergrade nearly always where they come in contact. A terrestrial group consists mainly of the three intergrading subspecies, *vagrans, elegans,* and *terrestris.* These two groups of subspecies are largely sympatric and no hybrids between them are known. This would be the simple story of two sympatric polytypic species if there were not additional complications. For instance, there is a population (*biscutatus*), somewhat intermediate between the aquatic and terrestrial groups, which intergrades with subspecies of both groups. This situation induces the author to lump the two species into one! To make matters worse, there is in the aquatic group an additional "subspecies" (*hammondi*) which intergrades with *couchii,* but is sympatric with *atratus* without signs of interbreeding. In spite of all the work done by Fitch, Fox, and others, it does not seem as if the analysis of this complicated group of garter snakes were completed. There must have been much former isolation, followed by secondary expansions, intergradations, and overlaps. To unravel this history would appear to be a worthwhile task.

[13] P. H. Greenwood. 1951. Evolution of the African Cichlid Fishes: The *Haplochromis* species-flock in Lake Victoria. Nature, **167**: 19–20.

[14] F. A. Pitelka. 1951. Speciation and ecologic distribution in American jays of the genus *Aphelocoma.* Univ. California Publ. Zool., **50**: 195–464, 14 pls., 21 figs.

[15] W. Fox. 1951. Relationships among the garter snakes of the *Thamnophis elegans* Rassenkreis. Univ. California Publ. Zool., **50**: 485–530, 13 figs.

Species structure in a flea.[16] The flea *Ctenophthalmus argytes,* one of the most common fleas of Europe, occurs on numerous species of mice, shrews, and moles. Still, there are now known in Europe alone twenty-one subspecies which the author arranges in six subspecies-groups, all strictly allopatric. Within each subspecies-group there are clines and a gradual change of populations. Between the subspecies-groups the change may be exceedingly abrupt. Jordan showed that in Normandy the western *celticus* group and the eastern *eurous* group approach each other to within a few hundred yards, without a sign of intergradation. In western Germany the *eurous* group meets the *argytes* group, but intergradation is limited to a long strip only about five miles in width, even though easy dispersal ought to be guaranteed by their mammalian hosts. These indeed puzzling facts are the basis of speculations of the author which reveal a complete ignorance of modern genetics. The facts indicate that the subspecies groups originated in geographical isolation from each other and acquired during this period of isolation such harmonious, well-balanced gene combinations that they do not break up on coming in contact with each other. There may also be selective mating as well as "intersubspecific" competition. The author's point that the borders of major subspecies (zones of secondary intergradation, Mayr, 1942) are often incredibly sharp in the absence of environmental barriers is well taken and deserves all possible emphasis and further study.

[16] F. Peus. 1950. Der Formenkreis des *Ctenophthalmus argytes* Heller (Insecta, Aphaniptera). Syllegomena biologica. Festschrift Kleinschmidt: 286–318.

Population structure.[17] In the box turtle (*Terrapene carolina*) there appears to be no territory defense, but individuals stay within a definite home range with a diameter of about 350 feet. The population of the study area was estimated to be between four and five turtles per acre, with juveniles constituting less than 10 per cent of the total. A long life of the adults and high mortality of the juveniles are indicated.

Anthropoid ancestors.[18] Le Gros Clark recently discussed the evolution of the hominids and anthropoids (review in EVOLUTION, **5**: 85). There is now available an impressive monograph of the Miocene hominoid finds from East Africa on which part of this discussion was based.

Phylogeny and systematics.[19] Author attempts to analyze the philosophical foundations of the systematic technique, as well as the use of these findings in the construction of phylogenies. Much is belabored that seems obvious, and many of the abstract discussions are very difficult to follow. However, there are many interesting illustrations of taxonomic problems taken from the author's experience in the systematics of Diptera.

[17] L. F. Stickel. 1950. Populations and home range relationships of the box turtle, *Terrapene c. carolina* (Linnaeus). Ecol. Monogr., **20**: 351–378.

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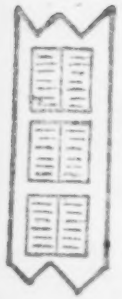

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